VIIS VIIMAST KAITSMIST

MARGOT SEPP
ORGANIC MATTER IN TEMPERATE LAKES – MONITORING AND CONNECTIONS WITH CATCHMENT
ORGAANILINE AINE PARASVÖÖTME JÄRVEDES – SEIRE NING SEOSED VALGALAGA
Professor **Tiina Nõges**
21. mai 2019

JIAYAN YE
QUANTITATIVE SCALING OF FOLIAGE PHOTOSYNTHETIC CHARACTERISTICS AND RELEASE OF CONSTITUTIVE AND INDUCED VOLATILES WITH SEVERITY OF BIOTIC STRESS
BIOOTILISE STRESSI KVANTITATIIVNE MÕJU LEHTEDE FOTOSÜNTEESILE NING KONSTITUTIIVSETE JA INDUTSEERITUD LENDUVATE ÜHENDITE EMISSIOONILE
Professor **Ülo Niinemets**
6. juuni 2019

KERSTI VENNIK
MEASUREMENTS AND SIMULATIONS OF RUT DEPTH DUE TO SINGLE AND MULTIPLE PASSES OF MILITARY VEHICLES ON TYPICAL ESTONIAN SOILS AND NATURAL RECOVERY OF RUTS
MILITAARSÕIDUKITE ÜLESÕITUDE TULEMUSENA KUJUNENUD ROOPASÜGAVUSE MÕÕTMINE JA MODELLEERIMINE EESTI MULDADEL NING ROOBASTE LOODUSLIK TAASTUMINE
Professor **Endla Reintam**, **Thomas Keller**, PhD (Rootsi Põllumajandusülikool), **Peeter Kukk**, PhD (Tartu Ülikool)
19. juuni 2019

KARIN NURME
ENCODING OF ENVIRONMENTAL HEAT BY THE SENSORY TRIAD OF INSECTS ANTENNAL THERMO- AND HYGRORECEPTOR NEURONS
KÕRGETE VÄLISTEMPERATUURIDE SENSOORNE KODEERIMINE PUTUKATE ANTENNAALSETE TERMO- JA HÜGRONEURONITE TRIAADI POOLT
Vanemteadur **Enno Merivee**, teadur **Anne Must**, dotsent **Ivar Sibul**
19. juuni 2019

KAIE METSAOTS
HOLISTIC DEVELOPMENT OF THE OIL SHALE REGION AS AN INDUSTRIAL HERITAGE, RECREATIONAL, SPORTS AND TOURISM DISTRICT
PÕLEVKIVIREGIOONI TERVIKLIK ARENDAMINE TÖÖSTUSPÄRANDI-, PUHKE-, SPORDI- JA TURISMIPIIRKONNANA
Professor **Kalev Sepp**
27. juuni 2019

ISSN 2382-7076
ISBN 978-9949-629-91-6 (trükis)
ISBN 978-9949-629-92-3 (pdf)

GUNNAR MOROZOV
CARBON AND NITROGEN FLUXES IN BIRCH AND GREY ALDER STANDS GROWING ON DIFFERENT SITES

Eesti Maaülikool
Estonian University of Life Sciences

CARBON AND NITROGEN FLUXES IN BIRCH AND GREY ALDER STANDS GROWING ON DIFFERENT SITES

SÜSINIKU- JA LÄMMASTIKUVOOD ERINEVATE KASVUKOHTADE KAASIKUTES JA HALL-LEPIKUTES

GUNNAR MOROZOV

A Thesis
for applying for the degree of Doctor of Philosophy in Forestry

Väitekiri
filosoofiadoktori kraadi taotlemiseks metsanduse erialal

Tartu 2019

Eesti Maaülikooli doktoritööd

Doctoral Theses of the Estonian University of Life Sciences

Eesti Maaülikool
Estonian University of Life Sciences

CARBON AND NITROGEN FLUXES IN BIRCH AND GREY ALDER STANDS GROWING ON DIFFERENT SITES

SÜSINIKU- JA LÄMMASTIKUVOOD ERINEVATE KASVUKOHTADE KAASIKUTES JA HALL-LEPIKUTES

GUNNAR MOROZOV

A Thesis
for applying for the degree of Doctor of Philosophy in Forestry

Väitekiri
filosoofiadoktori kraadi taotlemiseks metsanduse erialal

Tartu 2019

Institute of Forestry and Rural Engineering
Estonian University of Life Sciences

According to verdict No 6-14/9-2 of June 17, 2019, the Defence Board of PhD theses in Forestry of the Estonian University of Life Sciences has accepted the thesis for the defence of the degree of Doctor of Philosophy in Forestry.

Opponent: Professor **Leena Finér**, PhD
Natural Resources Institute Finland – Luke

Supervisor: Professor **Veiko Uri**, PhD
Institute of Forestry and Rural Engineering
Estonian University of Life Sciences

Defence of the thesis:
Estonian University of Life Sciences, room 2A1, Kreutzwaldi 5, Tartu
on August 21st, 2019, at 10:00.

The English language and the Estonian language in the thesis were revised by Mrs. Ester Jaigma.

Publication of this thesis is supported by the Estonian University of Life Sciences.

ISSN 2382-7076
ISBN 978-9949-629-91-6 (trükis)
ISBN 978-9949-629-92-3 (pdf)

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following five original publications (I-V). The articles are referred to in the text by their Roman numerals.

I **Morozov, G.**, Aosaar J., Varik, M., Becker, H., Lõhmus, K., Padari, A., Aun, K., Uri, V. (2019). Long-term dynamics of leaf and root decomposition and nitrogen release in a grey alder (*Alnus incana* (L.) *Moench*) and silver birch (*Betula pendula* Roth.) stands. Scandinavian Journal of Forest Research, 34(1): 12–25.

II Becker, H.; Aosaar, J., Varik, M., **Morozov, G.**, Aun, K., Mander, Ü., Soosaar, K., Uri, V. (2018). Annual net nitrogen mineralization and litter flux in well-drained downy birch, Norway spruce and Scots pine forest ecosystems. Silva Fennica, 52 (4): 1−18.

III Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., Soosaar, K., **Morozov, G.**, Ligi, K., Padari, A., Ostonen, I., Karoles, K. (2017). Carbon budgets in fertile grey alder (*Alnus incana* (L.) Moench.) stands of different ages. Forest Ecology and Management, 396: 55−67.

IV Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., **Morozov, G.**, Karoles, K. (2017). Ecosystems carbon budgets of differently aged downy birch stands growing on well-drained peatlands. Forest Ecology and Management, 399: 82−93.

V **Morozov, G.**, Aosaar, J., Varik, M., Becker, H., Aun, K., Lõhmus K.; Kukumägi, M., Uri, V. (20XX). The effect of thinning on annual net nitrogen mineralization and nitrogen leaching fluxes in silver birch and Scots pine stands. Submitted to Scandinavian Journal of Forest Research.

The contributions of the authors to the papers were as follows:

Paper	Original idea and study design	Data collection	Data analysis	Manuscript preparation
I	VU, KL	VU, **GM**	AP, **GM**, VU, KL	**GM**, VU, JA, MV, HB, KL, KA
II	VU	HB, **GM**, JA, MV	HB, VU, **GM**, JA, MV, KA,	HB, VU, **GM**, JA, MV, KA, ÜM, KS
III	VU	VU, MK, JA, MV, HB, **GM**,	VU, AP, MK, JA, MV, HB, **GM**,	VU, MK, JA, MV, HB, **GM**, AP, IO, KS, KLi, KK
IV	VU	VU, MK, JA, MV, HB, **GM**,	VU, MK, JA, MV, HB, **GM**,	VU, MK, JA, MV, HB, **GM**, KK
V	VU, GM	JA, MV, HB, KA, **GM**, VU	**GM**, VU	**GM**, VU, MK, HB, MV, KL, KA

AP – Allar Padari, HB – Hardo Becker, **GM – Gunnar Morozov**, IO – Ivika Ostonen, JA – Jürgen Aosaar, KA – Kristiina Aun, KK – Kalle Karoles, KL – Krista Lõhmus, KLi – Karli Ligi, KS – Kaido Soosaar, MK – Mai Kukumägi, MV – Mats Varik, VU – Veiko Uri, ÜM – Ülo Mander.

ABBREVIATIONS

AGB	Aboveground biomass
C	Carbon
CAI	Current annual increment
CAP	Current annual production
CRB	Coarse root biomass
DOC	Dissolved organic carbon
DON	Dissolved organic nitrogen
EC	Eddy covariance
FRB	Fine root biomass
FRP	Fine root production
GHG	Greenhouse gases
GLM	General linear model
K	Potassium
L	Leaching
MAI	Mean annual increment
N	Nitrogen
NEP	Net ecosystem production
NNM	Net nitrogen mineralization
NPP	Net primary production
P	Phosphorus
Rh	Heterotrophic respiration
Rs	Soil respiration
SOM	Soil organic matter
SWC	Soil water content
TOC	Total organic carbon
Ts	Soil temperature

1. INTRODUCTION

Increased CO_2 concentration in the atmosphere is one of crucial factors for global climate change, which has given rise to research interest in carbon (C) cycling in different ecosystems. According to the Paris Agreement (2015), governments should significantly reduce C emission and increase the share of bioenergy in the nearest future (UNFCCC eHandbook). In this aspect, it is essential to focus also on forest ecosystems at the global and regional levels since forests help to mitigate climate change (Schimel *et al.* 2001) by accumulating C in plant biomass as well as in soil (Cannell 1999, Mund *et al.* 2002, Pussinen *et al.* 2002, Hartmann *et al.* 2013; Körner 2017). In general, boreal and hemiboreal forests have been reported as ecosystems with high C sequestration capability (Dixon *et al.* 1994; Valentini *et al.* 2000; Liski *et al.* 2002, 2003; Gough *et al.* 2008). Thus, quantification and modelling of the main C fluxes of different forest ecosystems are highlighted. As changes in the C stocks may affect the balance between terrestrial and atmospheric C (Keith *et al.* 2009), clarification of C budgets at the ecosystem level is essential for understanding the driving forces behind the C cycle and sequestration capacity (Fang *et al.* 2007). However, C stocks and accumulation may be very variable due to the high heterogeneity of different forest ecosystems. Soil fertility is strongly related to soil nitrogen (N) content, which in turn affects forest C cycling. N is one of the essential nutrients and limited soil N restricts more effective C accumulation by forests (Feng *et al.* 2015).

Among different factors, also management has a great impact on the functioning of forest ecosystems, as well as on their C sequestration capacity. For ensuring relevant decision-making by foresters and policymakers, the knowledge of the effect of management should be improved in order to attain more effective C sequestration in forests.

When more effective C accumulation in forests is one way to reducing CO_2 level in the atmosphere, then the other way is reduction in C emission from fossil fuels. This assumes increasing the use of renewable energy sources, among them bioenergy. Also, this will increase the demand for various bioenergy sources in the nearest future and may intensify the management of forests. In this aspect, grey alder is recognized as a prospective fast growing tree species for energy forestry in Estonia (Uri

et al. 2002, 2003, 2009, 2011). In the other Nordic and Baltic countries grey alder is also known as a highly productive tree species in terms of biomass, owing to its potential as a source of renewable energy (Granhall & Verwijst 1994; Saarsalmi 1995; Rytter 1996; Telenius 1999; Miežite 2008; Hytönen & Saarsalmi 2015; Rytter & Rytter 2016). Moreover, *Alnus* species have the ability to symbiotically fix atmospheric N through *Frankia* bacteria and therefore are important for biological fertilization of soil (Granhall 1994). In forest ecosystems N_2 fixing trees may have a significant effect on the soil C pool, by increasing detritus inputs and contributing to humus formation (Binkley 2005). Moreover, as pointed out above, N availability in soil is one of the important factors limiting intensive C accumulation of forest trees (Feng *et al.* 2015). In the light of more intensive management of grey alder stands, C accumulation in these stands needed more profound investigation. Recent results have demonstrated that grey alder stands are able to accumulate a considerable amount of C both in biomass and in soil during a relatively short time period (Uri *et al.* 2011; 2014; Aosaar *et al.* 2013; Rytter & Rytter 2016), but C budgeting on an ecosystem level is still not attained. In the current study net ecosystem production (NEP) in five grey alder stands of different ages growing on fertile soils was estimated, by using C budgeting. It allowed to evaluate the effect of grey alder stands on regional C budget and to provide adequate information for foresters and policymakers (**III**).

Decomposition of organic matter is an important process for ensuring nutrient and C cycling in forest and it strongly related to ecosystem production. In some terrestrial ecosystems, more than 90% of net aboveground primary production may return to the soil in the form of litter, providing a major resource for soil decomposers (Swift *et al.* 1979). Thus, both above- and belowground plant litter are the main nutrient source for soil microorganisms (Persson 1979; Persson *et al.* 1980; Berg 1986) and may cover an essential part of the annual N demand of deciduous stands (Uri *et al.* 2011; Aosaar *et al.* 2016). Also a considerable C input in birch and alder stands will reach soil through above- and belowground litter (Varik *et al.* 2015; Uri *et al.* 2017ab).

Thus, from the point of view of C cycling in forest ecosystems, decomposition of organic matter plays an important role since the input of fresh organic C into soil is a major factor contributing to C accumulation, as well as to the heterotrophic respiration (Rh) flux

there. Moreover, clarification of root decomposition intensity has major methodological importance in terms of soil respiration measurement since the use of the trenching method to partition the components of Rh and autotrophic respiration in forest ecosystems is problematic (Kuzyakov 2006, Epron 2009, Varik *et al.* 2015, Kukumägi *et al.* 2017, Uri *et al.* 2017ab).

Although there is a number of studies on leaf and twig litter decomposition, among them birch and alder litter decomposition (Berg *et al.* 1982; Šlapokas and Granhall 1991ab; Dilly and Munch 1996, etc.), studies on root decomposition are scarce. Studies focusing on decomposition of both leaf litter and fine root litter in a complex manner have been unavailable.

Estimation of the decomposition dynamics of leaf litter and the litter of fine roots as well as coarser roots is necessary to provide new knowledge of CN cycling dynamics in forest ecosystems (**I**).

In northern latitudes, the amount of annual precipitation exceeds evapotranspiration and due to the resulting paludification process a significant share of the world's soil C pool is accumulated in peatlands (Gorham 1991; Martikainen *et al.* 1993). Draining of excessively moist soils in order to improve growth conditions for forests has been a common practice in northern regions, which has resulted in an increase of the productive forest land area. In Estonia, a considerable amount of forest area is located on organic soils and among them 15% (i.e. 328,000 ha) are classified under full-drained peatland forests (Yearbook Forests 2017). As a result of the long term drainage of swamps, there has emerged a novel specific site type, named "*Oxalis* full-drained swamp", according to local classification (Lõhmus 1984). Since forest drainage in Estonia has been quite intensive in the second half of the 20th century, it is estimated that about 70% of all Estonian peatlands are more or less affected by drainage (Paal *et al.* 1998). Drainage is extensive disturbance, which can cause significant shifts at the ecosystem level and can affect C balance between photosynthesis and soil respiration (Goulden *et al.* 1996; Lindroth *et al.* 1998; Hyvönen *et al.* 2007). Rh, derived from decomposition of litter and soil organic matter (SOM), is one of the largest C fluxes in ecosystems (Harmon *et al.* 2011) and is strongly favoured by drainage (Silvola *et al.* 1996). Assuming that CO_2 emission from forests on drained organic soils may be significantly increased due

to the intensive mineralization of SOM, these forests deserve special attention.

In the current thesis we analysed the dynamics of C cycling in downy birch stands of different ages, growing on long-term drained swamps. The main research question is: does the ecosystem of a drained downy birch forest act as a C sink or source, i.e. does more intensive C accumulation through increased biomass production exceed intensified C emission (**IV**)?

However, since N is strongly related to the C cycle (Feng *et al.* 2015), studies of the N cycle and N mineralization in forest ecosystems should be emphasized as well. N is one of the essential mineral elements limiting forest growth generally in the boreal region (Luo *et al.* 2004). N availability is an important factor affecting also C accumulation by plants and there is strong relationship between forest C and N cycling (Millard *et al.* 2007). Net nitrogen mineralization (NNM) is an essential flux in the whole N cycle of boreal and temperate forests (Zak *et al.* 1990; Goodale and Aber 2001; Lovett *et al.* 2002; Uri *et al.* 2008), and most of the N for plants uptake is produced by *in situ* mineralization of organic matter (Tate 1995).

Reduction in soil water content and improvement in soil aeration in drained peatlands promote conditions for more intensive NNM, which improves tree growth and influences ecosystem structure (Silins and Rothwell 1999). When NNM studies mostly focus on mineral soils in different forest ecosystems (Connell *et al.* 1995; Goodale and Aber 2001; Andersson *et al.* 2002; Lõhmus *et al.* 2002; Pajuste and Frey 2003; Uri *et al.* 2008, 2011; Becker *et al.* 2015, 2016), then relevant studies on organic soils are still quite scarce.

We studied the annual NNM flux in three main tree species forming most part of the stands growing in drained forest ecosystems in Estonia: Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and downy birch (*Betula pubescens*) (Becker *et al.* 2018). However, only the results about downy birch stand are included in the current thesis (**II**).

As already mentioned above, NNM is one of the key processes of N cycling in forest ecosystems and it is affected by several factors, among them tree species and soil type are the most crucial (Tietema

and Verstraten 1992; Lovett *et al.* 2002; Uri *et al.* 2008). Also forest management may have an impact on NNM intensity but this issue is still quite poorly studied. Obtained results are related mainly to clear-cutting (Kataja-aho *et al.* 2012; Becker *et al.* 2015) and stump harvesting (Becker *et al.* 2016). It is obvious that increased mineral N in soil enhances plants growth and forest productivity. On the other hand, the escalated NNM flux may lead to losses of N through leaching and gaseous emissions, unless additional N is not utilized by trees or other vegetation (Piirainen *et al.* 2007).

Thus, thinning may affect the NNM process in different ways. Due to increased soil temperature, NNM intensifies, attributing to increased production of trees. At the same time, the reduced organic aboveground litter input to soil may reduce annual NNM while the increased root litter input to soil (fine root litter from cut trees) may increase the NNM flux.

In the current study the effect of thinning on annual NNM intensity was studied in a young aged silver birch stand. And since N loss from the ecosystem is related to annual NNM intensity, also the effect of thinning on annual N leaching was estimated (**V**).

The present thesis is a synthesis of five papers. Two papers (**III** and **IV**) address C budgeting in two deciduous tree species; grey alder stands on fertile mineral soils and downy birch stands on fertile long-term drained organic soils. As decomposition of organic matter is an essential link between organic litter production, soil respiration and C accumulation in soil, paper **I** considers the decomposition dynamics of organic matter (leaf litter and fine root litter) in grey alder and silver birch stands. Moreover, the input and decomposition of organic matter affect fresh N input, which affects the annual NNM process. Two papers (**II** and **V**) focus on annual NNM as the main source of mineral N for plants uptake. Mineral N in soil strongly affects the productivity of trees and thereby C accumulation in stands. In paper **V** the effect of harvesting thinning on annual NNM is highlighted.

The current thesis addresses several novel aspects:

a) Studies focusing on the decomposition of both leaf litter and fine root litter in a complex manner so far unavailable;

b) a complete C budget was compiled for downy birch stands growing on well-drained fertile *Histosols*, considering that the literature does not offer similar studies;

c) an adequate C budget covering differently aged stands is the first this kind thorough study estimating all C fluxes in grey alder forest;

d) the short-term impact of commercial thinning on N mineralization and N leaching in birch stand has not been studied before, and the knowledge of this topic is scanty.

2. REVIEW OF THE LITERATURE

2.1. Leaf litter and fine root decomposition

Both above- and belowground plant litter plays a crucial role in different forest ecosystems. Organic litter is a main nutrient source for soil microorganisms (Persson 1979; Persson *et al.* 1980; Berg 1986) and may cover an essential part of the annual nitrogen (N) demand of deciduous stands (Uri *et al.* 2011; Aosaar *et al.* 2016). Also the main C input will reach soil through above- and belowground litter (Varik *et al.* 2015; Uri *et al.* 2017ab).

Studies on the decomposition of tree litter have been occasionally performed since the beginning of the 1980's in Great Britain (Bocock 1963; Chamier 1987), Canada (Lousier and Parkinson 1978; Aber and Melillo 1982; Melillo *et al.* 1982; Mellilo and Aber 1984; Melillo *et al.* 1989) and the U.S.A (Gosz *et al.* 1973; Meentemeyer 1978; Edmonds 1984; McClaugherty *et al.* 1985; Edmonds and Thomas 1995) and since the middle of the 1990's in Sweden (Berg and Staaf 1981; Berg *et al.* 1982; Staaf and Berg 1982; Berg *et al.* 1984; Berg 1986; Meentemeyer and Berg 1986; Berg *et al.* 1987; Berg 1988). In Estonia, the earliest experiments on aboveground tree litter decomposition were conducted in 1995 (Lõhmus and Ivask 1995).

When there are a number of studies on leaf and twig litter decomposition (Bocock 1963; Berg *et al.* 1982; Meentemeyer and Berg 1986; Chamier 1987; Šlapokas and Granhall 1991ab; Dilly and Munch 1996, etc.), then studies on root decomposition are scarce (Berg 1984; Lõhmus and Ivask 1995; Palviainen *et al.* 2004; Püttsepp *et al.* 2007). Studies focusing on decomposition of both leaf litter and fine root litter in a complex manner have been unavailable.

2.2. Net nitrogen mineralization and nutrient leaching

Available mineral N is produced from organic matter by in situ mineralization (Tate 1995), and net nitrogen mineralization (NNM) is one of the most important fluxes in the N cycle of boreal and temperate forests (Goodale and Aber 2001; Lovett *et al.* 2002). The NNM may

roughly vary between 20 kg ha^{-1} yr^{-1} and 200 kg ha^{-1} yr^{-1} and it covers a major part of the N demand of deciduous stands (Aber *et al.* 1989; Scott and Binkley 1997; Magill *et al.* 2000). NNM is affected by several factors, tree species and soil type being the most crucial among them (Tietema and Verstraten 1992; Lovett *et al.* 2002; Uri *et al.* 2008). Moreover, the intensity of NNM depends on many abiotic environmental factors like soil temperature, moisture, pH, etc., but also land use history may play a role (Zak *et al.* 1990; Goodale and Aber 2001; Lovett *et al.* 2002; Uri *et al.* 2008).

When NNM studies mostly focus on mineral soils in different forest ecosystems (Connell *et al.* 1995; Goodale and Aber 2001; Andersson *et al.* 2002; Lõhmus *et al.* 2002; Pajuste and Frey 2003; Uri *et al.* 2008, 2011; Becker *et al.* 2015, 2016), then relevant studies focusing on organic soils are still missing.

Although forest management evidently has some impact on NNM, the issue is still poorly studied and the results obtained pertain mainly to clear cutting (Kataja-aho *et al.* 2012; Becker *et al.* 2015) and stump harvesting (Becker *et al.* 2016). Moreover, the escalated NNM flux may lead to losses of N through leaching and gaseous emissions, unless additional N is assimilated by trees or other vegetation (Piirainen *et al.* 2007).

In terms of harvesting thinning, Thibodeau *et al.* (2000) suggested a possible limiting effect of commercial thinning on annual NNM. Fang *et al.* (2016) found high intensity thinning to (30-50%) increase annual NNM significantly due to elevated soil temperature and moisture content, which is the direct result of a decrease in canopy closure.

Usually, after thinning the remaining trees start to grow faster, which is mainly caused by reduced competition and increased available nutrients and other resources (Mäkinen and Isomäki 2004a). It has been found that thinning can redistribute available resources to enhance the vitality and increment of the retained trees (Mäkinen and Isomäki 2004bc; Mäkinen *et al.* 2006). Moreover, thinning changes the functioning of the forest ecosystem a great deal, including C and nutrient cycling.

However, despite the fact that thinning is a widely used tool in forest management, studies dealing with impacts of commercial thinning on the soil inorganic N stock as well as on soil N fluxes are scarce.

2.3. Carbon budgeting in grey alder and downy birch stands

Carbon (C) budgeting for different forest ecosystems is an actual topic in forest science at present due to increased atmospheric C and global climate change (Schimel *et al.* 2001; Walle *et al.* 2007; Verlinden *et al.* 2013; Wu *et al.* 2013). However, adequate assessment of the dynamics of C accumulation in forest ecosystems (both tree biomass and soil) requires an integrated approach i.e. empirical estimation of all main input and output C fluxes. Because of the large heterogeneity of forests, the cycling and accumulation of C in different forest ecosystems is highly variable, which makes the composing of regional C budgets complicated. General regional C budgets should be based on numerous key studies for different forest tree species and for different soils. However, complete C budgets for various forests are rare.

For estimation of C budget for forests, often the eddy covariance (EC) method is used. It is based on continuous measurements during a certain period, allowing estimation of C exchange between the ecosystem and the atmosphere, and is the most direct method for C cycling studies (Baldocchi 2014). However, this method only provides estimation of the quantity of input and output fluxes without detailed specification of the sources or sinks of the flux, which is its major shortcoming. The C budgeting method gives a good picture of the contribution of C accumulation in various ecosystem components, like trees, understorey plants, aboveground biomass, roots etc. (Uri *et al.* 2019). In the case of C budgeting, estimation of each C flux involves an error, which makes this method less accurate than EC is. From this aspect the direct method (EC) is considered to be a more reliable tool, in view of cumulated uncertainties involved in the indirect method (Meyer *et al.* 2013).

Studies of C budgets on the ecosystem's scale are important for understanding the driving forces behind the functioning of the C cycle and C sequestration capacity (Fang *et al.* 2007). However, relevant studies addressing alders and birches are still limited. For grey alder, extensive recent studies have demonstrated that these stands are able to accumulate a considerable amount of C both in biomass and soil during a relatively short time period (Uri *et al.* 2011, 2014; Aosaar *et al.* 2013; Rytter and Rytter 2016). However, this is but one part of the general picture, as far as little is known about C losses and final C balance. Soil heterotrophic respiration (Rh) is the main C output flux from forest

ecosystems and plays a crucial role. Yet only a few results are available about soil respiration in grey alder stands (Soosaar *et al.* 2011).

For C budgeting in silver birch stands, a thorough study was carried out in Estonia and the main C fluxes and storages were reported in two papers (Uri *et al.* 2012, Varik *et al.* 2013), followed by a concluding study with complete C budgets (Varik *et al.* 2015). Although C emissions from forests growing on drained peatlands have been studied taking account of different tree species (Minkkinen *et al.* 2007; Ojanen *et al.* 2010; Meyer *et al.* 2013), complete C budgeting for downy birch stands has not been published yet despite the extensive natural distribution area of this species on the Eurasian continent. Assuming that CO_2 emission from forests growing on drained organic soils may be significantly increased due to the intensive mineralization of soil organic matter (SOM), these forests deserve special attention. Rh, derived from decomposition of litter and SOM, is strongly favoured by drainage (Silvola *et al.* 1996). Drained and nutrient rich afforested organic soils are also potential sources of other greenhouse gases (GHG), contributing to global warming (Leppelt *et al.* 2014).

3. AIMS OF THE STUDY

Forests are essential carbon (C) sequestrating ecosystems and play an important role in the mitigation of climate changes on the global scale through accumulating atmospheric C. As carbon cycling and nitrogen (N) cycling in forests are strongly interrelated, integrated studies on forest ecosystem CN cycling are highlighted.

In the present thesis various C and N fluxes and storages were studied in grey alder, silver birch and downy birch stands. The working hypotheses and the main aims of the thesis are the following:

The main aims of the study are the following:

1. To estimate the decomposition dynamics of leaf litter and fine root litter in young grey alder and silver birch stands. A specific objective is to evaluate the suitability of the litterbag method as a tool to describe the rate of plant litter decomposition in fertile sites (**I**);

2. to analyse the dynamics of C cycling in differently aged downy birch stands on long-term drained swamps, by using the C budgeting method; also to estimate the annual NNM flux in downy birch stands growing at this site and to clarify the effect of NNM on C accumulation in stand (**IV** and **II**);

3. to estimate net ecosystem production (NEP) in five grey alder stands of different ages growing on fertile soils, by using C budgeting (**III**);

4. to estimate the effect of thinning on annual NNM intensity and annual nitrogen leaching in a young silver birch stand (**V**).

Hypotheses:

1. In similar soil conditions both the leaf litter and root litter of grey alder decompose more intensively, compared with the respective litter of silver birch, due to its higher nitrogen content and a more favourable C:N ratio **(I)**.

2. Downy birch stands growing on drained fertile *Histosols* act as effective C sinks owing to more favourable growing conditions and high biomass production which exceeds C loss through soil heterotrophic respiration **(IV)**. Also, high annual net nitrogen mineralization (NNM) intensity contributes to C accumulation through the high production of birch stands growing on well-drained fertile swamps **(II)**.

3. The C accumulation ability of grey alder stands is higher at a young age and will decrease with the maturing process. Because of their high biomass production ability, grey alder stands act as an effective C sink **(III)**.

4. After thinning in fertile birch stand, annual NNM will intensify as a consequence of increased soil temperature; also annual N leaching will increase because of the increased content of mineral nitrogen in soil **(V)**.

4. MATERIALS AND METHODS

4.1. Study sites (I, II, III, IV, V)

The data presented in the current thesis and in the original scientific publications are based on the different study sites of grey alder, downy birch and silver birch.

4.1.1. Grey alder (I, III)

Five grey alder stands aged between 7 and 38 years were used for the compile carbon budget chronosequence (Table 1) (**III**). All these stands grew in the highly fertile *Aegopodium* or the *Oxalis* site type according to the Estonian classification (Lõhmus 1984). The site history of these stands is the following: Agali and Kolleste 2 – naturally afforested previous agricultural land; Kolleste1, Ilmatsalu, Voopste – long-standing forest land. All these stands were located in South-East Estonia. The litter decomposition experiment (**I**) was carried out in a planted grey alder stand (Holvandi) which was established on an abandoned agricultural land (Uri *et al.* 2002, 2011). Since the fine root decomposition experiment lasted up to ten years, the stand characteristics of this stand are presented for two age stages (Table 1).

Table 1. Main characteristics of the studied grey alder stands. $D_{1.3}$ – breast height diameter of the stand.

Stand	Experiment	Age, yr	Average $D_{1.3}$, cm	Average height, m	Stand density, trees ha^{-1}	Basal area, m^2 ha^{-1}
Holvandi	Leaf and cellulose decomposition	3	-	2.1	14,020	-
Holvandi	Fine and coarser roots decomposition	9	5.2	8.5	8400	17.8

Stand	Experiment	Age, yr	Average $D_{1.3}$, cm	Average height, m	Stand density, trees ha^{-1}	Basal area, m^2 ha^{-1}
Kolleste 1	Carbon budgeting	7	3.0	6.5	18,750	13.3
Ilmatsalu		17	7.3	11.2	4630	19.5
Voopste		21	9.5	14.3	3280	23.1
Agali		32	15.4	17.3	1528	28.5
Kolleste 2		38	15.2	18.0	2734	49.5

4.1.2. Downy birch (II, IV)

The five downy birch stands of natural origin included in the study were aged 12 to 78 years (Table 2) (**II**). These stands grew on fertile *Oxalis* full-drained swamp soils (Lõhmus 1984) in Järvselja Experimental Forest District, South-East Estonia. The ditch drainage system was established 40-50 years earlier in all cases. From this dataset, a 30-year-old stand (DB-30) was involved in the net nitrogen mineralization (NNM) experiment (**II**).

Table 2. Main characteristics of the studied downy birch stands. $D_{1.3}$ – breast height diameter of the stand; NNM – net nitrogen mineralization experiment.

Stand	Carbon budgeting	NNM	Age, yr	Average $D_{1.3}$, cm	Average height, m	Stand density, trees ha^{-1}	Basal area, m^2 ha^{-1}
DB-12	+		12	7.9	12.0	2752	13.5
DB-24	+		24	11.5	14.7	1888	19.6
DB-30	+	+	30	13.7	15.2	1664	24.5
DB-38	+		38	11.9	14.6	1696	18.8
DB-78	+		78	17.9	19.3	768	19.4

4.1.3. Silver birch (I, V)

The silver birch stand with a long-term study history was used for two experiments (**I**, **V**). Leaf and fine root decomposition experiments were carried out at the stage of young age of the stand (**I**) and an NNM study (**V**) was performed on same stand when it was 20 years old (Table 3). The stand is located in South-East Estonia and growing in the *Oxalis* site type (Lõhmus 1984). It is of natural origin and was regenerated on former agricultural land (Uri *et al.* 2007, 2008).

Table 3. Characteristics of the studied silver birch stands. $D_{1.3}$ – breast height diameter of the stand; NNM – net nitrogen mineralization experiment.

Stand	Experiment	Age, yrs	Average $D_{1.3}$, cm	Average height, m	Stand density, trees ha^{-1}	Basal area, m^2 ha^{-1}
Kambja, control		8	3.2	6.6	11,600	8.6
		Decomposition				
Kambja, control	NNM	20	11.0	18.2	2600	24.5
Kambja, thinned	NNM	20	11.9	20.3	1840	20.3

4.2 Leaf and root decomposition experiments.

Both leaf and root litter decomposition experiments were carried out at two sites: a young grey alder stand and a young silver birch stand (ch. 4.1.1 and 4.1.3).

For both tree species, a similar experimental design was used. The leaves for incubation were collected from litter traps of the same stands in the same year when the experiment was initiated and were dried in a laboratory oven at +70 °C to constant weight. Dried leaf litter was then divided into 80 individual samples (for both species). The samples were placed into 15x15 cm litterbags made of 1 mm polypropylene mesh. Each individual sample was weighed to 0.01 g with a weight ranging from 1.7 to 2.8 g for grey alder and from 2.0 to 2.1 g for silver birch.

A plastic label with the number of the sample was inserted into the litterbag for further identification. Altogether 80 leaf litterbags were divided between 8 strings, with 10 litterbags each. The experiment with leaf litter was initiated in November 1996 for grey alder and in October 2004 for silver birch **(I)**.

The decomposition experiment with the fine (d<2mm) and coarser roots (2≤d<5mm) of grey alder and silver birch were initiated in August 2002 and in November 2004, respectively. The roots for the experiments were collected in the summer of the current year and from the same stands, using a spade for taking soil samples from a depth of up to 20 cm. The roots were separated and gently washed with tap water to remove adhering soil particles. The roots were then divided into different fractions (fine roots d<2 mm and coarser roots 2≤d<5 mm) in the laboratory. The roots that were dead or decaying as well as the roots of the understorey vegetation were removed. Only the roots that seemed alive at the time of collecting were stored for further experiment. The roots were dried to an air dry state at 70 °C, hacked into approximately 1 cm pieces and placed in nylon fabric litterbags with dimensions of 5x5 cm and with a mesh size of 0.14 mm. The weight of the roots in every bag was set exactly at 1.000 g. Five samples from every fraction were separated for initial chemical analyses as well for estimation of ash content. The samples were incubated in the soil at a depth of 5-10 cm.

In the grey alder experiment root samples were installed along 4 transects, each transect included two strings, with 20 litterbags attached to each (one row with d<2mm and the other with 2<d<5 mm roots). In the silver birch experiment there were 5 transects, each transect had also two strings, with 16 litterbags attached to each. In total 160 bags with roots (80 of d<2mm and 80 of 2<d<5 mm) were buried in the experimental area for both tree species.

4.3. Net nitrogen mineralization experiments (II, V)

For both NNM experiments, the buried polyethylene bag method was applied (Eno 1960; Adams *et al.* 1989; Hart *et al.* 1994; Uri *et al.* 2003, 2008, 2011; Becker 2016). Polyethylene bags with a thickness of 18 μm were used, which ensures the permeability of gases (O_2, CO_2, N_2, etc.) but prevents leaching and addition of soluble N, as well as N uptake by plants. There are several *in situ* methods to estimate N

mineralization, but the methods of buried bags or the covered cylinders are two among the most common (Hanselman *et al.* 2004; Duran *et al.* 2012). One month is the optimal period during which the changes in mineral nitrogen concentration are assumed to take place (Adams *et al.* 1989). Simultaneously with the incubation, also initial samples were taken from the surrounding next to the incubated sample site. All samples were taken randomly from the upper 10 cm soil mineral layer with a cylindrical soil corer (Ø 48 mm). The internal diameter of the inner part of the corer was 1.6 mm larger than the cutting edge to avoid compression of the soil. For incubation, the samples were sealed in the polyethylene bags and placed in the same hole from where they had been taken. In the downy birch stand growing on dried peatland the NNM experiment was carried out from May 2014 to June 2015 (**II**) and in the thinning study areas, NNM was studied from July 2016 to October 2017 (**V**). In both experiments sampling was done monthly throughout the year, except for the period when the soil was frozen. At each sampling session 24 samples were taken from each treatment. Both the incubated and the initial samples from each sampling were collected separately and gathered in three composite samples. All samples were transported to the laboratory on the same day.

Annual monthly NNM was calculated as the difference in N content between the incubated samples and the initial samples. Bulk density was used to calculate mineralized N in the upper 10 cm soil layer (Uri *et al.* 2008; Becker *et al.* 2016).

4.4. Nitrogen and carbon leaching (III, V)

Nitrogen leaching and carbon leaching were estimated by using stainless steel plate lysimeters (**III**, **V**). In both studied grey alder stands (32-year-old Agali and 21-year-old Voopste) 10 lysimeters were installed at a depth of 40 cm in the soil. In the thinning study 14 lysimeters (7 at the thinned site + 7 at the control site) were installed for estimation of N leaching in the silver birch stand (**V**). The collecting area of one lysimeter was 627 cm^2 and the lysimeters were connected via plastic tubes to a water collecting plastic canister (6000 ml). Percolated water was collected monthly in all studies, except for the winter period, when the soil was frozen.

4.5. Carbon budgeting (III, IV)

The C budget for the studied stands was compiled by balancing the data of the input and output fluxes of C. A well-known approach for defining net ecosystem production (NEP) was used, which is the difference between net primary production (NPP) and loss of C through heterotrophic respiration (Rh) and leaching (L) (Clark *et al.* 2001, Lovett *et al.* 2006, Meyer *et al.* 2013):

$$NEP=NPP-(Rh+L) \quad (2)$$

NEP represents the rate at which C is accumulated in the ecosystem, and is the main parameter characterizing forest as a C sink or as a C source (Chapin *et al.* 2006, Waring and Running 2007). NPP was calculated by summing the annual increments of the aboveground ecosystem compartments (trees, understorey plants) and the annual increments of the belowground ecosystem compartments (tree coarse root system, fine roots, roots and rhizomes of the understorey). A detailed description of estimation of different C fluxes is presented in papers (**III**, **IV**). A positive value of NEP indicates the net transfer of C from the atmosphere to forest when the ecosystem acts as a C sink. A negative value of NEP implies the net transfer of C from forest to the atmosphere when the ecosystem is a C source.

4.6. Soil analysis

For soil analyses, soil pits to a depth of 1.0 m were dug for every study stand or site (**I**, **II**, **III**, **IV**, and **V**). Pit locations were selected randomly over the site. The soil profile was described and the soil type was determined according to the WRB (2006). To estimate soil bulk density, a stainless cylinder 50 cm^3 was used. Bulk density samples were taken to a depth of 50 cm with a 10 cm interval. The samples were dried at 105 °C to constant weight and weighed to 0.001 g. For soil chemical analyses, subsamples were taken from 10-15 random points per sample plot to a depth of 30 cm with a cylindrical soil corer (Ø 40 mm). The samples were taken from different depths (0–10, 10–20, 20–30 cm soil layers). The subsamples formed a composite sample and taken to the laboratory. The content of C and nutrients in the different soil layers was analysed in three replicates.

4.7 Chemical analysis

The Tecator ASN 3313 was employed for testing the soil samples for N according to Kjeldahl. Soil NO_2^-, NO_3^- and NH_4^+ were determined by flow injection analysis with the Tecator ASN 65-32/84 and the Tecator ASN 65-31/84. Available phosphorus in the extraction solution was determined by flow injection analysis with the use of the Tecator ASTN 9/84 and the content of available potassium was determined from the same solution by the flame photometric method. Available (exchangeable) Ca and Mg were determined by using 1 mol L^{-1} NH_4OAc extracting solution buffered at pH 7. Soil magnesium content was determined by flow injection analysis with the Tecator ASTN 90/92. Calcium was determined from the same solution by the flame photometric method. Soil pH in 1 M KCl suspensions was measured at a ratio of 10 g : 25 ml. To test soil for the C content of oven-dried samples, the dry combustion method was used with the varioMAX CNS elemental analyzer (ELEMENTAR, Germany).

To test the plant material for C content in the oven-dried samples, the dry combustion method was used with the varioMAX CNS elemental analyser (ELEMENTAR, Germany). The analyses were carried out at the Biochemistry Laboratory of the Estonian University of Life Sciences.

Water samples were analysed for NH_4^+, NO_2^-, NO_3^- at the Biochemistry Laboratory of the Estonian University of Life Sciences and dissolved organic nitrogen (DON) and dissolved organic carbon (DOC), at the Laboratory of the Estonian Environmental Research Centre by using standard methods for water research (APHA 1989).

4.8. Statistical analysis

Normality of variables was checked using the Lilliefors and Shapiro-Wilk's tests. To analyse the effect of the treatment factors on the response variables, ANOVA was applied. ANOVA assumptions - normality, homogeneity of group variances and nonsignificant relationship between the group means and the standard deviations - were checked. For multiple comparisons of the means in case the assumptions were satisfied, the t-test was employed to compare the two group means. Correlation matrix was used to estimate relationships. The Wilcoxon Matched Pairs test was applied to compare the medians. The Tukey HSD

test was employed to perform multiple post-hoc comparisons between mean C and nutrient content for the different fractions.

Soil respiration data were transformed to normality by log-transformation. To examine the effect of stand age and treatment (trenching) on soil respiration (Rs) or heterotrophic respiration (Rh), soil temperature (Ts) and soil water content (SWC), a repeated measure analysis of variance (ANOVA) was performed using the general linear model (GLM) procedure. In the case of significant effects ($P < 0.05$), the means were compared with Tukey's HSD test.

Linear and allometric models were employed for estimating relationships. The measure of the fit of the models was based on the adjusted coefficient of determination (R^2) and the p-value (P).

In all cases the level of significance $\alpha=0.05$ was accepted. The software STATISTICA 7.0 was employed.

5. RESULTS

5.1. Leaf and root decomposition and nitrogen release in grey alder and silver birch stands (I)

The decomposition rate for the leaves of silver birch and grey alder throughout the four study years is described by an exponential function (Fig. 1; Table 2, **I**).

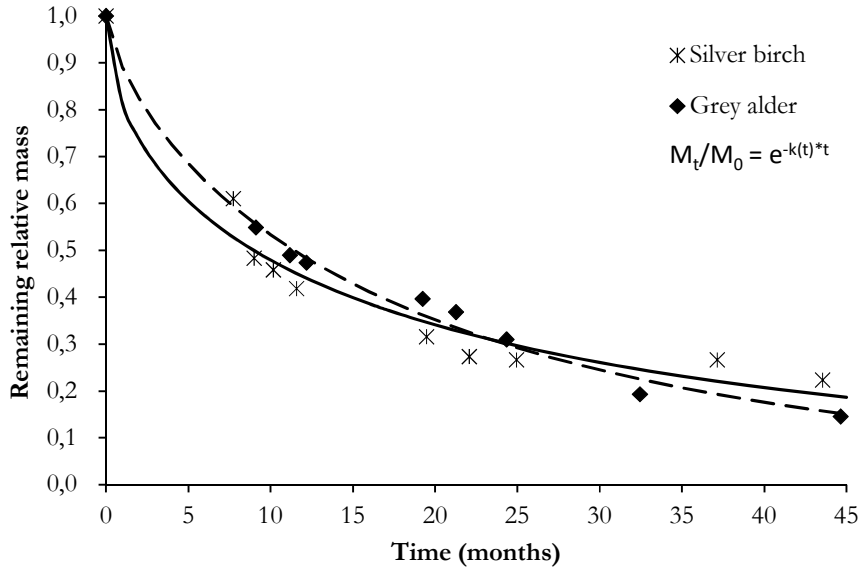


Figure 1. The dynamics of the remaining relative dry mass of silver birch and grey alder leaf decomposition over 3 years of the experiment (**I**).

The general pattern of the decomposition dynamics of leaf litter was similar for both studied tree species. In the first 12 months, a significant loss of initial mass occurred, at 57% and 53%, for silver birch and grey alder, respectively (Fig. 1). Decomposition slowed down thereafter and in the second year, the remaining amount of litter was almost similar, (Fig. 1).

After three years of decomposition, approximately 20% of leaf mass was still left for both species, compared to the initial mass. At the end of the experiments, the remaining relative mass of the silver birch and grey alder leaves was 19% and 15%, respectively. The silver birch leaves lost

more relative mass compared to the grey alder leaves during first study year, later on the mass of the silver birch leaves decreased more slowly than the mass of the grey alder leaves.

The initial content of nitrogen (N) in the incubated leaves was significantly lower in the silver birch samples (Fig. 2, **I** and Table 3, **I**) and remained lower throughout the experiment compared to the grey alder leaves. However, the dynamics of N content in the leaves was similar for both species: it increased during the first 20 months and declined thereafter (Fig. 2, **I**). This pattern lasted till month 25 for silver birch and month 32 for grey alder, followed by a slight increase.

Samples of α-cellulose were incubated in the topsoil as well as on soil surface in late autumn (November). Intensive decomposition started in the following spring and the mass loss of the samples was described by a linear model (Fig. 3, **I**). The decomposition of cellulose in the soil was fast: after 32 weeks only about 20% of the initial mass was left and after 41 weeks cellulose had almost disappeared from the litterbags. The cellulose samples incubated on soil surface lost less than 10% of the initial mass after 45 weeks of decomposition. At 75 weeks of incubation, the decomposition process intensified and by the end of the second year practically no cellulose was left on soil surface. The decomposition rate of cellulose on soil surface in the second year was similar to the decomposition rate of cellulose in the soil in the first year. The overall rate of decomposition of the samples incubated in the soil was almost twice as high.

At the beginning of the experiment with cellulose, N content in the samples was zero; 7 months after incubation, N was present both in the samples from the soil and from soil surface (Table 4, **I**). N content in the cellulose sheets from the soil was 7 times as large as in the cellulose sheets from soil surface indicating higher abundance of decomposers.

Decomposition of cellulose sheets can be characterized by the increase in N at the beginning of the experiment and the decrease in the later stage.

For grey alder roots, the pattern of decomposition was similar for both the $d<2$mm and $2<d<5$mm fractions. The decomposition dynamics

can be characterized by the same exponential function as is used for decomposition of leaves (Table 2, **I**).

The initial mass of fine (<2mm) and coarser roots (2-5mm) decreased during 64 weeks of decomposition by 64% and 57%, respectively (Fig. 4, **I**). Thereafter, the rate of decomposition decreased markedly. However, after nearly 11 years from the initiation of the experiment, the mass of the remaining fine and coarser roots made up 11% and 9% of their initial mass, respectively. Also the roots had sustained their physical form at the end of the experiment.

Although the dynamic pattern characterizing the decrease of mass was similar for both types of grey alder roots, their rate of decomposition was statistically different ($\ln(c)$ $p = 0.045$): coarser roots tended to lose their mass faster than fine roots (Fig. 4, **I**) (pairwise t-test, $p < 0.01$).

For silver birch roots at the confidence level 95%, root diameter seemed to be a nonsignificant factor, yet it was significant at the confidence level 90%.

Within the first 100 weeks of the decomposition experiment, the loss of initial mass was more intensive in the fraction of coarser roots for both silver birch and grey alder (Fig. 4, **I** and Fig. 5, **I**).

The largest difference between these fractions occurred in the relative remaining mass after one year from the initiation of the experiments (Fig. 4, **I** and Fig. 5, **I**). Thereafter the difference between the two fractions of roots for both species declined and eventually levelled out in the late phase of the experiment ($p = 0.532$).

After approximately 9 years of decomposition of the fine and coarser roots of silver birch, the irrelative remaining mass was about 21% and 20% of the initial value, respectively.

According to ANOVA, the role of tree species in the decomposition of the roots of both fractions was insignificant – the respective fractions of silver birch and grey alder roots decomposed following a similar dynamics.

The difference in N content between the roots of silver birch and grey alder was significant (Table 3, **I** and Table 5, **I**). However, the dynamics of N content in decomposable fine roots showed a similar trend: it started to increase in the early phase of the experiment, peaking halfway of the study, and declined steadily thereafter but remaining still higher than in the initial samples. Unlike the decomposition experiment with fine roots, the decomposition of coarser roots showed a trend where N content increased steadily throughout the experiment.

Comparison of N release from the decomposed litter demonstrated that the main share of the annual N input to soil originated from leaves while the contribution of roots was modest (Table 6, **I**).

5.2. Carbon budgets in fertile grey alder stands of different ages

Woody biomass production of trees

Annual C accumulation in stands was strongly related to the biomass production of trees. The general growth dynamics of the studied stands was in accordance with the data of the Estonian grey alder yield table (Uri *et al.* 2014). Only the oldest mature stand (Kolleste 2) did demonstrate exceptionally high annual stem mass production, which significantly exceeded the corresponding values of the yield table (Fig. 2, **III**). Current annual woody biomass production (CAP) in all studied stands fluctuated significantly between the study years, which was probably caused by weather conditions. Comparison of leafless CAP across all stands revealed that it was higher in 2011 and 2014 than in 2013 and 2015, respectively (Table 4, **III**).

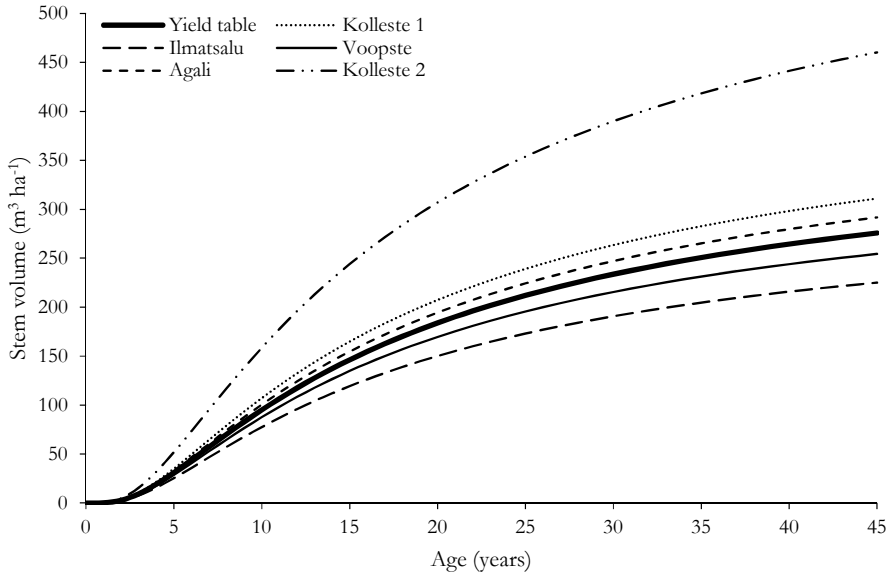


Figure 2. The dynamics of stem volume in the studied time-series stands in comparison with the Estonian grey alder yield table (**III**).

Aboveground litter

In the studied grey alder stands 0.9 – 2.5 t C ha^{-1} reached the soil through aboveground litter annually and the main share of annual aboveground litter was formed of leaf litter (Table 5, **III**). The share of branches was negligible in the youngest stand: ca 1% in all study years. In the other stands it varied from 2% to 15%. Variability occurred across the studied sites; the total annual C flux to soil via litter fall was smaller in the youngest stand but the difference was not statistically significant (LSD test; P=0.07) (Table 5, **III**).

Herbaceous understorey

The aboveground biomass of herbaceous plants was not dependent on either stand age or density, varying from 0.7 to 1.1 t ha^{-1} in 2013 (Table 6, **III**). However, the aboveground biomass of the herbaceous vegetation in the Voopste stand in 2013 (1.14 t ha^{-1}) was significantly larger than in the Kolleste 2 and Ilmatsalu stands (t-test; $P<0.05$). The biomass of the belowground part of herbaceous plants was similar, roughly 0.4 t ha^{-1}, in all stands.

Carbon input into soil via the fine roots

Although no correlation was found between fine root (d<2mm) biomass (FRB) and stand age (P>0.05), FRB tended to be lower in younger stands (Table 7, **III**). The majority of the fine roots (80%) were located in the upper 20 cm topsoil layer in all stands and FRB declined with increasing soil depth. The annual production of fine roots (FRP) was similar in all stands with the exception of one stand (Agali) where the current value was almost twice as low, which can be explained by the lower density of this stand (Table 4, **III** and Table 7, **III**).

The turnover of fine roots decreased with the ageing of the stand while the lifespan of the fine roots increased. The mass of dead fine roots was of the same magnitude in all studied stands, i.e. roughly 0.6 t ha^{-1} (Table 7, **III**). The annual belowground organic C input into soil via fine roots ranged between 0.4 and 0.9 t C ha^{-1} yr^{-1} in 2013 (Table 7, **III**).

Leaching of organic carbon

The annual leaching of total organic carbon (TOC) in the studied stands (Agali and Voopste) was low (26 and 19 kg ha^{-1} yr^{-1}, respectively). The major share of TOC leached in spring after the melting of snow (Fig. 3, **III**). Based on the data from Voopste and Agali, we assumed that the flux of TOC was negligible also in the other studied stands.

Soil respiration and the microclimate

The seasonal dynamics of soil respiration (Rs) (Fig. 4, **III**) and heterotrophic respiration (Rh) in all stands showed a similar pattern following changes in Ts. The Ts was the main driver of seasonal variation in the soil CO_2 efflux. The Ts described 80 to 95% of variation in Rs; only in the youngest stand did Ts describe 67% of Rs in 2013 (Fig. 5, **III**). The same applied to Rh: in 2014, Ts described 88 to 94% of the variation in Rh; in 2013 the descriptive force of Ts was somewhat lower, at 53-81%.

Trenching treatment did not affect Ts (P>0.05) but increased soil moisture on average by 20% across the stands and over the measurement period (P<0.05). Soil moisture fluctuated markedly throughout the growing season ranging from 11% to 69% in the studied stands.

The efflux of CO_2 varied significantly between the stands (Table 8, **III**). Over 2013 and 2014, modelled annual Rs ranged from 5.3 to 9.9 t C ha^{-1} yr^{-1} and annual Rh ranged from 2.6 to 5.8 t C ha^{-1} yr^{-1}. The relative contribution of Rh to Rs for the period from May to November varied irrespective of stand age, with the highest contribution of Rh to Rs in the youngest stand (Table 8, **III**).

Carbon budgeting

In general, the studied grey alder stands acted as C sequestration ecosystems, i.e. in most cases NEP was positive, remaining in the range of -1.98 to +4.1 t C ha^{-1} yr^{-1}. The main source of C emission was Rh, the share of C leaching from the ecosystem was negligible. In the youngest stand a strong effect of the year was evident: the stand was an efficient C emitting ecosystem one year (-1.98 t C ha^{-1} yr^{-1}) and a C accumulating system in the following year (+0.93 t C ha^{-1} yr^{-1}) (Table 4, **III**). The NEP was higher in the old Agali stand (34-35 years) than in the younger stands (19-24 years), which can be attributed to high NPP and low Rh. The oldest grey alder stand was a modest C source, emitting 0.8 t C ha^{-1} yr^{-1}.

Table 4. The carbon budgets of the grey alder stands of different ages (**III**).

		Kolleste 1		Ilmat-salu	Voopste		Agali		Kolleste 2
	Stand age (years)	9	10	19	23	24	34	35	40
	Flux (t C ha^{-1} yr^{-1})								
	Plant aboveground								
1	Leafless tree biomass increment	1.02	2.30	1.48	1.78	2.12	2.66	3.34	1.50
2	Leaf litter	1.02	1.13	1.66	1.77	1.86	1.96	1.7	1.86
3	Branches +other litter	0.01	0.00	0.04	0.09	0.70	0.26	0.56	0.14
4	Herbaceous understorey production	0.44	0.46	0.29	0.49	0.70	0.41	0.61	0.33

		Kolleste 1		Ilmat-salu	Voopste		Agali		Kolleste 2
	Plants belowground								
5	Coarse root biomass increment	0.26	0.58	0.31	0.37	0.44	0.56	0.70	0.32
6	Tree fine root production	0.73	0.81	0.90	0.59	1.17	0.41	0.43	0.87
7	Understorey root and rhizome production	0.15	0.15	0.17	0.20	0.36	0.18	0.26	0.15
	Output								
8	Heterotrophic respiration (C output)	5.6	4.5	2.7	4.9	4.7	2.6	2.9	5.8
9	TOC leaching	n.e	n.e	n.e	0.02	0.02	0.03	0.01	n.e
	Soil								
10	C input = (2)+(3)+(4)+-(6)+(7)	2.35	2.55	3.06	3.14	4.79	3.22	3.56	3.35
11	Soil C exchange = (10)-(8)	-3.25	-1.95	0.36	-1.76	0.09	0.62	0.66	-2.45
	Productivity								
12	NPP = (1)+(2)+(4)+-(5)+(6)+(7)	3.62	5.43	4.81	5.20	6.65	6.18	7.04	5.03
13	NEP = (12)-(8+9)	-1.98	0.93	2.11	0.30	1.95	3.58	4.14	-0.77

5.3. Carbon budgets of differently aged downy birch stands growing on well-drained peatlands

Carbon accumulation in woody biomass production

The allometric model described well both the aboveground biomass and the stem mass of the downy birch trees on the basis of breast height diameter (Fig. 3). However, for better estimation, individual parameters of the model were used for stands of different ages (Table 3, **IV**). The share of stem mass in the total aboveground biomass of the model trees was very stable, ranging between 84 and 87%.

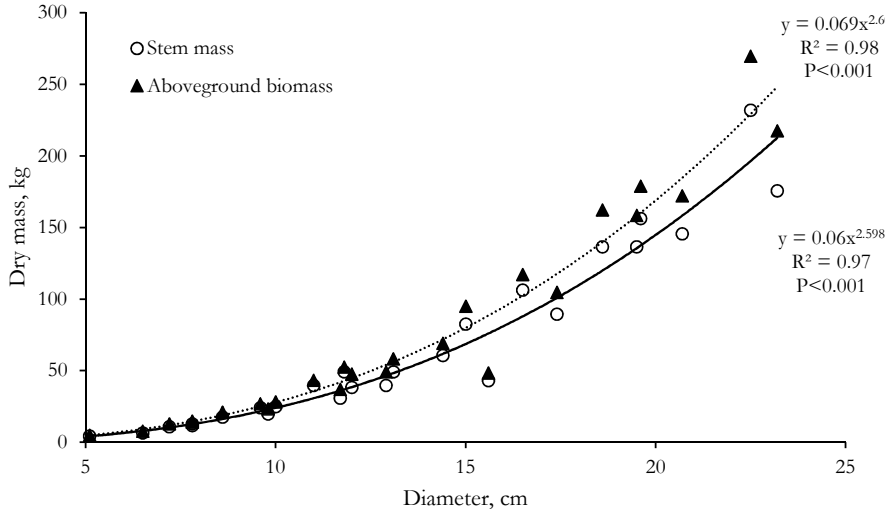


Figure 3. The regression model of aboveground woody biomass and stem mass on the basis of the downy birch model trees (n=26) (**III**).

Both the current annual increment (CAI) and the mean annual increment (MAI) of stemwood demonstrated higher values for the youngest stands and a considerable decrease for the older stands (Table 4, **IV**).

The weighted average C content of aboveground woody biomass for the studied downy birch stands was 47.6%. Variation in the C content of the different fractions of the downy birch trees ranged between 47 and 51%, being the highest (51.0%) in twigs and the lowest (47.0%) in stemwood (t-test) (Table 5, **IV**). The corresponding C content values were used for calculation of the C fluxes and storages.

Woody biomass production increased until a stand age of roughly 40 years and decreased in the oldest stand. Hence, C accumulation in woody biomass was the most intensive in the young and middle-aged stands (Table 6, **IV**). However, the C storage in standing woody biomass increased markedly with stand age (Table 4).

The coarse root biomass (CRB) of an average model tree in the 30-year-old downy birch stand was 26.2 kg. The stump core and the roots with the largest diameter ($d \geq 10$mm) accounted for 27% and 56% of total CRB, respectively. The corresponding shares of the root fractions $5 \leq d < 10$ mm and $2 \leq d < 5$ mm were similar (7% and 6%, respectively). The share of the belowground part in aboveground woody biomass accounted for 28%, which was applied for calculation of the total CRB of the stands.

Aboveground litter

The annual C flux into soil via litter fall was of the same magnitude in all stands, being the smallest (1.5 t C ha^{-1} yr^{-1}) in the oldest stand (Table 7, **IV**). The litter flux was the largest in the 30-year-old stand but differed statistically only from that of the oldest stand (Tukey test; $P<0.05$).

Leaf litter formed the main share of the organic C flux into soil; the proportion of branches was modest in all stands. The average C content of leaf litter over the whole study period was 49.6%. Thus taking roughly 50% for average C content in this case should be relevant.

Herbaceous understorey

The biomass of the herbaceous understorey plants decreased with stand age ($R=0.88$; $P<0.05$). The belowground to aboveground biomass ratio was variable for the stands of different ages (Table 7, **IV**). Average C content in the above- and belowground biomass of the herbaceous plants was 43.5% and 46.2%, respectively.

Carbon input into soil via fine roots

Fine root biomass (FRB) was of the same magnitude across the studied stands, being roughly 1.5 t ha^{-1}, except for the oldest stand (DB-78) (Table 7, **IV**). Neither FRB nor fine root production (FRP) was dependent on stand age (ANOVA, $F=0.99$ and $P=0.12$, respectively).

Although stand density was lower in the oldest stand, its FRB was of the same magnitude as in the other stands, average FRB per tree increased in the older stands. Fine root turnover rate varied between 1 and 2 yr^{-1} for the studied stands, which indicates that the total fine root biomass is renewed during one year. The C content did not differ significantly between fine and coarse roots and stemwood (Table 5) and the annual C flux into soil via decomposing fine roots was roughly 1 t C ha^{-1} yr^{-1}.

Soil respiration and microclimate

The seasonal dynamics (from May to November) of soil temperature (Ts) was quite similar for all studied stands (data not shown). The lowest mean monthly Ts across all stands was recorded in November, and the highest in August. Trenching did not affect Ts.

Throughout the growing season, soil moisture fluctuated roughly between 20% and 60% in the studied stands, except for July in the 38- and 78-year-old stands where the soil was drier compared with the other stands ($P<0.05$); in May the soil of the youngest stand was saturated with water and its moisture was markedly higher than the soil of the other stands ($P<0.05$) (Fig. 3, **IV**).

Regarding the different stands, the soil was drier in the 38- and 78-year-old stands (23±2.1% and 32±3.1%, respectively) compared with the 12-, 24-, and 30-year-old stands (50±4.4%, 46±1.9% and 53±1.6%, respectively) ($P<0.05$). Soil moisture was similar in the control and trenched plots in the 24- and 30-year-old stands. In the 12-, 38- and 78-year-old stands, soil moisture was higher in the trenched plots than in the control plots ($P<0.05$). However, among these stands, the moisture values improved the regression model only in the case of the youngest stand.

The seasonal dynamics of Rs and Rh showed a similar pattern in all stands following changes in Ts (Fig. 4, **IV**).

The CO_2 efflux was different between the stands; measured respiration rates in the 24-year-old stand tended to be lower compared to the other stands, however, a significant difference in Rs rates was found only between the 24-year-old and the 30-year-old stands ($P<0.05$). Also mean Rh was significantly lower in the 24-year-old stand than in the 30- and

38-year-old stands ($P<0.05$). No significant difference was found in the respiration rates between the other stands. Cumulative annual Rs was 7.4-8.8 t C ha^{-1} yr^{-1} and cumulative annual Rh was 4.7-6.2 t C ha^{-1} yr^{-1}, with the highest values for the middle-aged stands (Table 8, **IV**). At the same time, mean soil C emission did not differ significantly between the stands of different ages (ANOVA, t-test $P>0.05$). The relative contribution of Rh to Rs varied between 0.60 and 0.70 irrespective of stand age.

Carbon budgets

The values of the net ecosystem production (NEP) in the downy birch stands decreased from the youngest to the oldest stand (from +3 to -0.95 t C ha^{-1} yr^{-1}) (Table 6, **IV**). The C was primarily accumulated in tree biomass and the largest C input flux into the soil originated from aboveground litter. Both the aboveground and belowground litter (FRP) fluxes were of the same magnitude in all studied stands of different ages and the C input through the annual production of the herbaceous understorey plants was modest (Table 6).

The annual heterotrophic soil respiration (Rh) flux exceeded the annual organic C input into the soil (Table 6) in all stands irrespective of stand age or depth of the soil organic layer. This indicates continuous mineralization of peat and a decrease of the soil C storage.

Table 5. Carbon input and output fluxes and net ecosystem production (NEP) in the downy birch stands growing on Histosols (**IV**).

Flux, t C ha^{-1} yr^{-1}	Stand				
	DB-12	DB-24	DB-30	DB-38	DB-78
Plant aboveground					
(1) Leafless tree biomass increment	3.84	3.20	3.11	2.55	1.69
(2) Leaf litter	1.63	1.50	1.65	1.62	1.17
(3) Herbaceous understorey production	0.14	0.19	0.17	0.10	0.05
Plant belowground					
(4) Coarse root biomass increment	0.79	0.63	0.71	0.47	0.27

(5) Tree fine root production	0.89	1.07	1.19	1.48	0.92
(6) Understorey root and rhizome production	0.43	0.19	0.08	0.07	0.05
Soil					
(7) C output (Heterotrophic respiration)	4.7	5.1	5.5	6.2	5.1
(8) C input = (2) + (3) + (5) + (6)	3.09	2.95	3.09	3.27	2.19
(9) Soil C exchange = (8) - (7)	-1.61	-2.15	-2.41	-2.93	-2.91
Productivity					
(10) NPP = (1) + (2) + (3) + (4) + (5) + (6)	7.72	6.78	6.91	6.29	4.15
(11) NEP = (10) - (7)	3.02	1.68	1.41	0.09	-0.95

5.4. Annual net nitrogen mineralization in a well-drained downy birch forest ecosystem

The total soil N pool in the downy birch stand growing on *Drainic Eutric Histosols* was high and was estimated roughly at 5 t N ha^{-1} in the upper 10 cm soil layer.

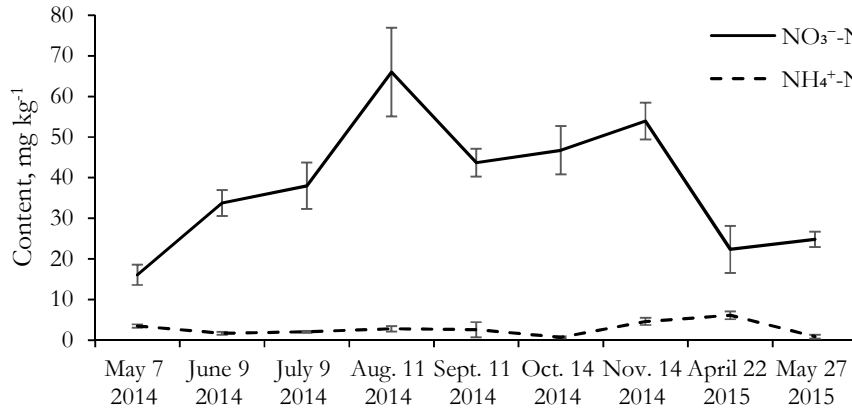


Figure 4. Mean content of soil NO_3^--N and NH_4^+-N in the upper 10 cm soil layer of downy birch stand. Bars indicate standard error values, n=8 (24 replicates pooled by three) (**II**).

Soil mineral N content peaked in August and November, amounting almost to 70 mg kg^{-1} and the highest share of soil mineral N was formed of NO_3^--N, (Fig. 4), NH_4^+-N was almost missing.

In the studied birch stand the peak of nitrogen net nitrogen mineralization (NNM) was in July 2014 (t-test, $P<0.05$), when NNM intensity exceeded 120 mg kg^{-1} N day^{-1} and another peak (109 mg kg^{-1} N day^{-1}) occurred in June 2015 (t-test, $P<0.05$) (Fig. 5). The rate of net nitrification was high whereas ammonification rate was even negative in seven months.

There was positive correlation between NNM intensity and soil temperature ($r=0.78$, $P=0.013$). However, when we considered the net nitrification and net ammonification processes separately, positive correlation occurred only between soil temperature and net nitrification ($r=0.80$, $P=0.009$). There was no correlation between soil pH and NNM intensity or between soil moisture content and NNM intensity. Annual cumulative NNM was estimated almost at 130 kg ha^{-1} yr^{-1}, which made up 2.4% of the soil N pool of the upper 0–10 cm.

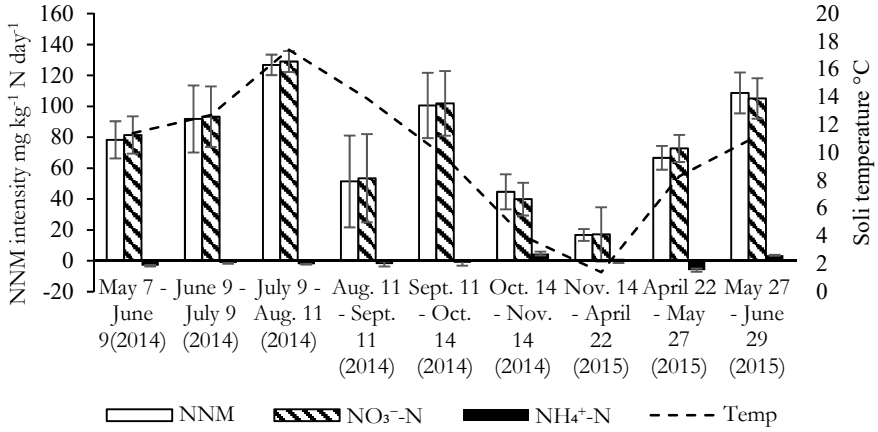


Figure 5. Dynamics of monthly average soil temperature in the upper 10 cm soil layer and the dynamics of net nitrogen mineralization (NNM) intensity (mg kg^{-1} N day^{-1}) in the downy birch stand in 2014-2015. Bars indicate the values of standard error (**II**).

5.5. Effect of harvesting thinning on net nitrogen mineralization and nitrogen leaching in silver birch stand (V)

Dynamics of soil mineral nitrogen content

During the first year after thinning (2016) the content of soil mineral N fluctuated monthly in the thinned plot; in the control plot its content across the studied months was more stable (Fig. 1, **V**). However, the share of mineral N for the upper 10 cm soil layer in the control and thinned plots was quite low, varying between 1.9 and 4.0 mg kg^{-1} and between 1.7 and 5.7 mg kg^{-1}, respectively. Average soil mineral N content was higher in the thinned plot, showing a statistically significant difference ($P<0.05$) for four months (Fig. 1, **V**). Soil mineral N content was substantially higher at a younger stand age (8 years), varying between 26.7 and 35.5 mg kg^{-1} (Uri *et al.* 2008). Thereafter it started to decrease and was at the same level in 2014 (0.14 and 2.62 mg kg^{-1}) as in 2016-2017.

Soil mineral N content peaked both in the control and thinned plots in April 2017, being 4.0 and 5.7 mg kg^{-1}, respectively. During the second post-thinning vegetation period (2017) it decreased steadily and was at its lowest in August. When in the first post-thinning year (2016) soil mineral N content in the thinned plot fluctuated from month to month, then in 2017 its values were more stable. However, although the relative change of mineral N content between the studied months was marked, then its absolute values changed only 2-3 mg kg^{-1}. Regarding the different forms of mineral N, ammonium N (NH^+_4) was dominating in the soil, making up 83.2% to 100% and 59.9 to 100% of total mineral N in the control and thinned plots during the whole study period, respectively.

The average soil ammonium N content was slightly higher in the control plot, but this difference did not reach statistical significance ($P=0.84$, Welsh t-test). However, the average content of nitrate N revealed a statistically significant difference ($P<0.05$); the average content of NO^-_3 in the soil of the thinned plot was higher throughout the study period.

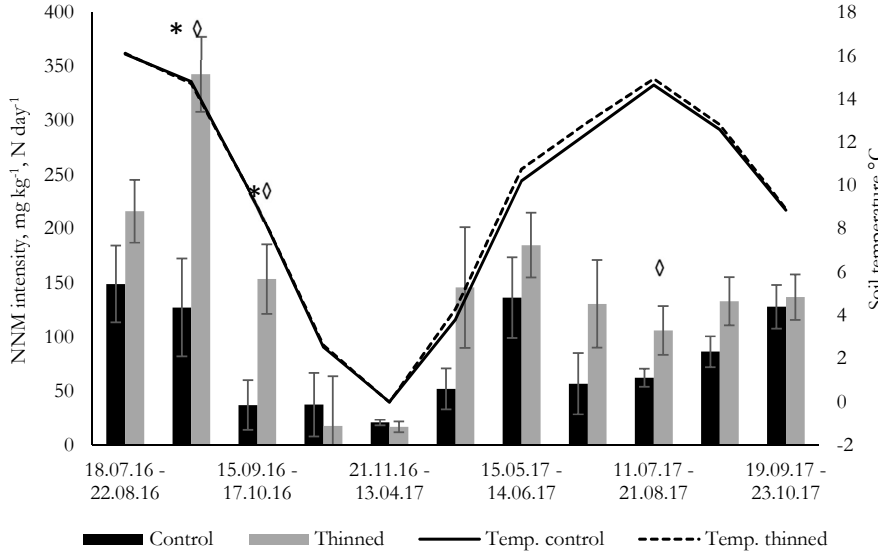
Dynamics of annual net nitrogen mineralization

The dynamics of the NNM flux in the silver birch stand over the whole study period (2016-2017) was different in the control and thinned plots (Fig. 6, **V**). However, the difference was larger in the first year

after thinning (2016) and levelled out in the following year (2017). In most cases monthly NNM was more intensive in the thinned plot, being significantly higher during the three studied months (Fig. 6, **V**). Thinning was a significant factor which affected the annual NNM flux during the first post-thinning year (ANOVA, $F=17.1$; $P<0.001$). Thinning increased the total annual NNM flux which was 24 kg ha^{-1} higher in the thinned plot. When the annual flux of ammonification was practically similar in the control and thinned plots, then the nitrification flux was almost threefold higher in the thinned plot (41.7 versus 113.0 mg kg^{-1} N day^{-1}) (Table 3, **V**). The dynamics of annual ammonification was similar in both study plots ($P=0.49$).

NNM intensity peaked in late summer (August-September) in the thinned plot while its monthly fluctuation was much lower and smoother in the control plot (Fig. 6, **V**).

The first NNM experiment in this silver birch stand was carried out in 2004-2005 (Uri *et al.* 2008) and a repeat NNM study was performed from April 2014 to May 2015 with the use of the same above described polyethylene bags method. The 13-year period of stand development (from 2004 to 2017) revealed a decrease of the annual NNM flux: when in the young stage the annual NNM flux was 99 kg ha^{-1} yr^{-1} for the upper 10 cm soil layer (Uri *et al.* 2008), then ten years later (2014-2015) it was only 52 kg ha^{-1} yr^{-1}. In the current study (2016-2017) the NNM flux in the control plot demonstrated a decrease and was estimated at only 30 kg ha^{-1} yr^{-1} (Table 3, **V**).



* - statistically significant difference (two-tail); ◊ - statistically significant difference (one-tail)

Figure 6. Dynamics of net nitrogen mineralization intensity (mg kg^{-1} N day^{-1}) and soil temperature in the upper 10 cm soil layer of the silver birch stand, control versus thinned. Bars indicate standard error (**V**).

There was strong correlation between soil temperature and NNM intensity (mg kg^{-1} N day^{-1}) during the first post-thinning year (2016) both in the control plot (r=0.90) and in the thinned plot (r=0.88) (Spearman Rank Correlation). However, in the following study year (2017) this relationship was obliterated (Fig. 6, **V**). Significant relationship was not established between monthly NNM intensity and soil moisture content (P>0.05) in the control or in the thinned plot.

Environmental factors

Thinning affected soil volumetric moisture content, which was significantly lower in the thinned plot during almost all studied months, except for spring 2017 (**V**). The dynamics of soil temperature was practically similar in the thinned and control plots (Fig. 6, **V**) except for only one month in mid-summer 2017 when average soil temperature was significantly higher in the thinned plot.

Generally, the dynamics of soil pH followed the same pattern in the control and thinned plots (Fig. 5, **V**). However, at the end of the

vegetation period 2016 there was a significant difference in soil pH between the studied plots.

The long term dynamics of soil pH in upper 0-10 cm soil layer demonstrated a slight decrease; when in 2004 average soil pH was 5.60, then in 2014 it was 5.47; in 2016-2017 soil pH was 5.38 in the control plot and 5.43 in the thinned plot.

Nitrogen leaching

The annual flux of N leaching was generally low, but it was higher in the control plot than in the thinned plot, 5.5 versus 2.3 kg N ha^{-1} yr^{-1}, respectively. Also the amount of percolated water demonstrated a different pattern for the two plots, 2100 t ha^{-1} yr^{-1} for the control plot and 930 t ha^{-1} yr^{-1} for the thinned plot.

Nitrate nitrogen (NO_3^--N) and organic dissolved N (DON) made up most of leached N (Fig. 7, **V**). Nitrate N made up 39% of all leached N in the control plot and 45% in the thinned plot. The share of DON in leached soil water was 57% in the control plot and 52% in the thinned plot. The share of ammonium N was relatively low, accounting for 4% and 3% of total leached N in the control plot and in the thinned plot, respectively. In both variants N leaching peaked in early spring (April).

6. DISCUSSION

6.1. Decomposition and nitrogen release of tree litter in grey alder and silver birch stands (I)

The dynamics of leaf litter decomposition was similar for both studied tree species, following a negative exponential function, which is in good accordance with several earlier results (Šlapokas and Granhall 1991b; Berg 2000; Vares 2001; Prescott 2010).

During the first year of experiment, the decrease of the relative mass of leaf litter was intensive for both tree species, reaching roughly 60% of the initial mass and slowing down thereafter (Fig. 1, **I**). According to Coûteaux *et al.* (1995), litter mass loss takes place in two phases – mineralization and humification of litter, and the leaching of soluble into the soil. Thus, the huge amount of mass loss in the early phase of decomposition can be attributed to the leaching process, where water soluble substances are washed out of litter, and to the degradation of free unshielded holocellulose (Berg 2000). In the last phase (from month 25 to month 37) the loss of relative mass was between 3 and 4% for both substrates.

It was hypothesized that the leaf litter of grey alder decomposes faster because of its higher N content. The N content and the C:N ratio of decomposing organic matter has a strong effect on decomposition (Šlapokas 1991b; Scott and Binkley 1997); high level of initial N content increases decomposition rate (Maloney and Lamberti 1995; Dilly and Munch 1996; Horodecki and Jagodziński 2017). Despite the significant difference in the quality of the decomposing substrate in terms of N content, the dynamics of mass loss was similar for both species ($P>0.05$). Evidently, N content in the litter of silver birch leaves was sufficient, exceeding the threshold for ensuring intensive decomposition. Also their higher content of cellulose, compared to that in grey alder leaves, may have induced higher mass loss of silver birch leaves in the first year, as cellulose decomposes faster than lignin.

The decomposition experiment with cellulose sheets was included in the study since cellulose decomposition indicates potential soil fertility and soil microbial activity. As expected, α-cellulose decomposition in the

soil was very rapid: slightly over half of the initial mass was lost after half a year of decomposition (Fig. 3, **I**), indicating the high activity of decomposers.

The decomposition of the cellulose samples on soil surface had been slower, one year after incubation about 80% of the initial mass was left. Later on the situation changed: cellulose started to decompose rapidly and after two years only 7% of the initial mass was left. The reasons for such an abrupt change in the decomposition rate can be manifold, e.g. weather conditions, contact with the soil and presence and activity of decomposers. In the first year, the decomposition of cellulose on soil surface was most probably inhibited by the low abundance of decomposers. Because of poor contact with the soil, there occurred a lag phase. In the second year, the decomposition rate was similar both on soil surface and in the soil. (Fig. 3, **I**).

Both studied species (grey alder and silver birch) had a similar decomposition pattern of roots with different diameters (fine roots $d<2$mm and coarser $2\leq d<5$mm roots) (Figs. 4 and 5, **I**). However, in both cases, fine roots lost their initial mass more slowly than coarser roots. This can be explained by the early loss of cortical material, which is easily degraded and will be more abundant in roots with a larger diameter. A number of other root decomposition studies have shown similar results (McClaugherty *et al.* 1984; Fan and Guo 2010, Goebel *et al.* 2011; Sun et al 2013; Xiong *et al.* 2013; Sun *et al.* 2016).

The effect of tree species on decomposition dynamics was not revealed: roots with the same diameter decomposed at a similar rate for both species. Although N content and the C:N ratio varied significantly among the substrates (Table 2, **I**), there was no significant difference in the decomposition rate.

The share of the N input in the aboveground and belowground litter fluxes may vary to a large extent in different forest ecosystems. In the current study, the N flux from aboveground litter into the soil was the main N input from decomposed organic matter for both studied fast growing tree species. This can be attributed to the significantly larger mass (Table 6, **I**) and faster decomposition of leaf litter versus root litter (Figs. 1, 4 and 5, **I**). From the point of view of N budget for both

stands, the N input from fine roots plays a modest role (Uri *et al.* 2011; Aosaar *et al.* 2016).

In the current study we found root residues in litterbags even as late as 9 (for silver birch) and 11 years (for grey alder) after incubation while they had maintained their physical form as roots. It is evident that in natural conditions both fine roots (d<2mm) as well as the roots of the coarser fraction (2<d<5 mm) decompose into an amorphous mass and disappear in a few years, which was confirmed also by our fine root studies at the same sites. According to earlier studies, FRB was a stable parameter, being 870 and 810 kg ha^{-1} in the 10-year-old stand and 17-year-old stand, respectively (Uri *et al.* 2002, Aosaar *et al.* 2013). At the same time, fine root necromass in the soil was modest for both sampling periods (190 and 110 kg ha^{-1}, respectively). Taking into account that annual FRP was 530 kg ha^{-1} (Aosaar *et al.* 2013) and the total decomposition of fine roots takes more than 10 years, fine root necromass in the soil must be enormous. Actually, it was low, indicating that the real decomposition dynamics of fine roots in natural conditions is much faster than it is in litterbags.

The litterbag method is widely used for decomposition experiments and, like any other method, it has advantages as well as disadvantages. According to an extensive review, a majority of litter decomposition studies (87%) were conducted with the buried litterbag method (Silver & Miya 2001). It is a basic method for this kind of experiments and is relatively easy to use. However, its main disadvantage is that the environmental conditions affecting decomposition are different from natural conditions (Šlapokas and Granhall 1991a). Several authors have noted that the activity of some soil macrofauna, especially earthworms, isopods, gastropods and millipedes, is more or less excluded. Mesh size alters microbial and physical processes in the course of decomposition, large mesh size excludes meso- and macrofauna, whereas smaller mesh size impedes the exchange of gas, water, nutrients and microorganisms (Lecerf 2017).

The difference between decomposition rates in free soil and in the litterbag is probably more significant for fertile soils where the effect of earthworms is more apparent, like it revealed in our case. The abundance of earthworms is related to soil type and moisture, pH and organic matter content (Edwards and Bohlen 1996).

6.2. Carbon budgets in fertile grey alder (*Alnus incana* (L.) Moench.) stands of different ages

Carbon accumulation of trees

Continuous measurements in the studied stands demonstrated a significant effect of the year, i.e. weather conditions, on the biomass production of the stands and hence on annual C accumulation in them (Table 4, **III**). For example, the biomass production of all studied stands was lower in 2013 which can be explained by droughty conditions (Table 4, **III**). This is in good accordance with earlier studies, which demonstrated that very dry summers may drastically decrease the CAP of grey alder stands (Uri *et al.* 2009; Aosaar *et al.* 2013). Also Rytter (2013) pointed out that water limitation suppresses both the above- and belowground biomass production of young grey alder plants In the rainy year (2014), the CAP of all stands was one of the highest over the study period (Table 4, **III**).

Both stem mass and production in the oldest stand (Kolleste 2) was unexpectedly high (Fig. 1, **III**) compared to the average growing stock presented in the Estonian grey alder yield table (Uri *et al.* 2014). This was mainly due to higher stand density; the number of trees was almost twice as high as the average value for grey alder stands of the same age (Uri *et al.* 2014) owing to dense tree groups within the stand. High stand density also can be explained by the fact that almost all grey alder stands in Estonia are unmanaged. High diversity of natural grey alder stands is a common feature which explains why forest growth models are always broad generalizations. Yet the growth dynamics of the other four stands harmonizes with the corresponding values of the Estonian grey alder growth model (Fig. 1, **III**; Table 3, **III**).

Aboveground litter and herbaceous understorey vegetation

The annual leaf litter flux was of the same magnitude across the stands, except for the youngest one where the amount of litter was approximately twice as low as in the other stands (Table 5, **III**). The average annual litter fall across all studied stands over the three study years was 3.5 t ha^{-1} yr^{-1}, which is higher than the mean annual total litter flux reported in an extensive Finnish study: 2.3 t ha^{-1} yr^{-1} for both grey alder and black alder stands (Raulo & Hokkanen 1989). In deciduous stands, both foliage

mass and leaf area increase substantially during the early developmental stage, reaching optimal level and stabilizing thereafter. In the case of grey alder, this is consistent with relevant literature data (Rytter *et al.* 1989; Rytter & Rytter 2016), as well with our earlier results (Uri *et al.* 2002; 2009), according to which the leaf mass of grey alder stands stabilizes at the age of 5-10 years. Annual leaf mass production may fluctuate depending on weather conditions during the growth period; there was found a negative impact of drought on foliage mass (Uri *et al.* 2009; Aosaar *et al.* 2016).

The biomass production of the herbaceous understorey, accounting for 10-16% of the annual NPP of the stands, was not related to stand age and the C input from herbaceous aboveground biomass was relatively modest (Table 9, **III**). The share of the aboveground biomass of herbaceous plants exceeded the share of belowground biomass, which is contrary to the results from silver birch stands (Varik *et al.* 2015) where the belowground biomass of herbaceous plants exceeded significantly their aboveground biomass.

Fine roots

Belowground biomass, particularly the fine roots, are essential for their contribution to C cycling in forest ecosystems (Brunner & Godbold 2007; Finer *et al.* 2011). The belowground part is the main bottleneck in studying forest ecosystem's C cycling (Leppälammi-Kujansuu *et al.* 2014) as well as in compiling C budgets. The FRB in the studied stands ranged from 1.1 t ha^{-1} to 2.6 t ha^{-1}, being the smallest in the youngest stand (Table 7, **III**), whose value is close to an earlier result for a 10-year-old grey alder stand (0.87 t ha^{-1}) (Aosaar *et al.* 2013). This is consistent with a Latvian study where the average FRB in mineral soils of 4-9-year-old grey alder stands was estimated at 1.2±0.4 t ha^{-1} (Bardulis *et al.* 2015).

Fine root production (FRP) may vary a great deal depending predominant on the tree species, soil condition and stand age (Nadelhoffer & Raich 1992; Eissenstat & Yanai 1997). Also the method used affects the result of FRP, in the present study we used the root mesh method (Hirano *et al.* 2009; Lukac & Godbold 2010). We assumed that the annual C input through fine root litter was equal with fine root annual production. In the current study the estimated FRP was of same magnitude in all studied stands, i.e. it was not dependent on stand age (Table 7, **III**). Only

one stand, Agali, was exceptional where lower FRP can be explained by lower stand density. Regarding the FRP of grey alder, only a few results are available (Uri *et al.* 2011; Aosaar *et al.* 2013; Rytter 2013).

However, in our study the annual C input into soil via fine root litter may be underestimated since we sampled root meshes once per year, in October. According to Rytter (2013), quite a large part of short-living finest roots (<1 mm) may have very high turnover rate (5-6 yr^{-1}). We considered our possible underestimation of FRP to be 15-40% according to the data for a 17-year-old grey alder stand presented in Aosaar *et al.* (2013), while Rytter (2013) estimated fine root turnover for 3-year-old seedlings in a lysimeter experiment. Thus the estimated FRP in the studied stands is most probably an underestimation and the actual C input into soil via root litter may be even larger.

Carbon output fluxes

In the present study both total soil respiration (Rs) and heterotrophic soil respiration (Rh), varied across the grey alder stands of different ages and showed no clear trend in relation to stand age (Table 8, **III**). The Rh contributed the most to Rs in the youngest stand (Table 8, **III**) where annual C emission in 2013 was comparable to that of the oldest stand (5.6 versus 5.8 t C ha^{-1} yr^{-1}). It should be noted that the youngest stand was a naturally generated stand growing in a previous clear-cut area where harvesting residues (dying root systems, stumps and other organic decomposing material) contributed to Rh. Moreover, also the soil microclimate there (1.7 ºC higher mean Ts of the growing season in 2013 than in 2014, and generally high moisture level) favored the decomposition of organic matter. Soil temperature and moisture are known to be the main climatic factors associated with the soil CO_2 efflux (Luo & Zhou 2006; Bahn *et al.* 2010; Gaumont-Guay *et al.* 2014). Contrary to our expectations, soil respiration was significantly lower in two stands – the middle-aged (Ilmatsalu) stand and the mature (Agali) stand. Low C:N ratio and strong correlation with soil temperature should lead to higher soil respiration. However, there are also other factors which affect respiration. For example, respiration has been found to be related to FRB or FRP (Lee & Jose 2003; Saiz *et al.* 2006; Knohl *et al.* 2008; Tang *et al.* 2009; Kukumägi *et al.* 2016). In the Agali stand, both FRB and FRP were significantly lower compared with the other stands (Table 7, **III**). However, after relating the annual soil respiration flux to

stand density, these differences in soil respiration between the Ilmatsalu and Agali stands disappeared.

In the present study, the estimated annual C leaching from the Agali and Voopste stands was quite small and leached C made up only a minor proportion of the total C budget. Although C leaching was not directly measured for the three other stands, this did not affect the compiling of C budgets since TOC leaching was negligible.

Carbon budgeting

Several studies report that the magnitude of a forest C sink or C source varies with stand age (Law *et al.* 2003; Kolari *et al.* 2004; Pregitzer & Euskirchen 2004). According to our earlier study of grey alder (Uri *et al.* 2014), C accumulation in the grey alder forest ecosystem is more intensive in younger and middle-aged stands, which is due to the dynamics pattern of biomass production.

Annual NEP in the studied stands fluctuated significantly during the 5-year study period and annual NEP depended on weather conditions in the current year rather than on stand age (Table 9, **III**). The effect of weather, especially precipitation and drought, may be revealed when one follows the annual biomass increment of grey alders (Uri *et al.* 2009; Aosaar *et al.* 2013).

According to literature data, mature stands can become weak C sinks or even sources of C (Goulden *et al.* 1996; Lindroth *et al.* 1998; Kriiska *et al.* 2019) since their annual biomass production decreases. On the other hand, soil Rh is another factor that plays an essential role here and stand age is reported to be one factor affecting soil respiration. However, different authors have reported an increase (Wiseman & Seiler 2004), or a decrease (Saiz *et al.* 2006), in soil respiration, but also non-linear responses of soil respiration to stand age (Wang *et al.* 2002; Tang *et al.* 2009; Varik *et al.* 2015). The high NEP in the mature (Agali) stand can be attributed to high production, on the one hand, and to the low Rh fluxes, on the other. Also, the oldest stand, Kolleste 2, showed still vigorous growth but the high Rh flux changed this forest to a C emitting ecosystem. However, all studied stands demonstrated considerable fluctuation in NPP during the 5-year study period (Table 4, **III**).

The effect of the year on the C budget was demonstrated in the youngest (Kolleste 1) stand where the leafless CAP for the two sequential years differed more than two times, turning the stand from a C source (-2 t C ha^{-1} yr^{-1}) into a C sink in the second year (+1 t C ha^{-1} yr^{-1}). Since Kolleste 1 was of sprout origin, then the share of the belowground fraction may have been higher and hence also annual NEP may be slightly underestimated. Yet soil C exchange was negative in both years in this forest (Table 9, **III**), which can evidently be attributed to its land use history, as mentioned above. As our earlier studies have shown (Uri *et al.* 2011; 2014; Aosaar *et al.* 2013), land use history is crucial in terms of capturing C by soil. The Agali stand was considered a first generation alder forest growing on previous agricultural land where soil C exchange was highly positive, i.e. annual C capture by the soil was 0.65 t C ha^{-1} yr^{-1}. It is slightly lower than our earlier estimates for grey alder stands (0.84-1.2 t C ha^{-1} yr^{-1}) (Aosaar *et al.* 2013; Uri *et al.* 2014) but fits well the range of the model-based estimation (0.34-0.68 t C ha^{-1} yr^{-1}) reported by Rytter & Rytter (2016). Negative soil C exchange is probably a temporary phenomenon for alder stands growing on a mineral soil. The C emission presumes presence of a large organic C pool in soil, which is a typical situation after stand harvesting. In the youngest stand the soil C storage was the largest (178 t C ha^{-1} yr^{-1}) (Table 2, **III**) among the five studied stands. Furthermore, it exceeded the average soil C storage of Estonian grey alder stands belonging to the same age class (5-10-years) (Uri *et al.* 2014). Intensive Rh in the oldest (Kolleste 2) stand is difficult to explain since its soil C pool was the lowest (82.5 t C ha^{-1} yr^{-1}). Without doubt, soil type, fertility, water regime, etc. are also crucial factors affecting the soil C pool as well as the C sequester (Paul *et al.* 2003). However, the C budget for grey alder stands of different ages was positive in most cases, i.e. these stands were acting as C sinks.

The annual organic C input flux into soil (in the form of aboveground and belowground litter) was of similar magnitude in the studied stands, being between 3 and 3.5 t C ha^{-1} yr^{-1}, except for the youngest stand where it was lower (2.4 t C ha^{-1} yr^{-1}). The C flux from leaf litter and annual FRP accounted for 30-54% of the annual NPP of the stands and showed no correlation with stand age.

The Rh is a key factor affecting the stand C economy pattern and this flux was largely stable and varied less than annual NPP for the two consecutive study years. It seems that compared with Rh, annual NPP

is more sensitive to the weather conditions of a particular year. For instance, in the middle-aged Voopste stand, NEP fluctuated between two consecutive years roughly at 2 t C ha^{-1} yr^{-1} while the annual Rh flux remained practically at the same level (**III**).

6.3. Carbon budgets of differently aged downy birch stands growing on well-drained peatland

Carbon accumulation in woody biomass

The growth pattern of the studied downy birch stands demonstrated intensive biomass production at the young stage and decline with increasing stand age (Table 4, **IV**), which is a common dynamic forest growth pattern. Growth peaked in the 30-year-old stand with a standing volume of 193 m^3 ha^{-1}. It remained in the range of reported aboveground biomass (AGB) values of 62 and 212 t ha^{-1} for 21- and 37-year-old downy birch stands growing on cutaway peatland, respectively (Hytönen & Aro 2012). In the present study, the mean annual stemwood increment (MAI) of the stands was between 4.2 and 6.4 m^3 ha^{-1} yr^{-1} for the young and middle-age of stands (Table 4, **IV**), which can be considered a high value for downy birch.

We established strong correlation (R^2>0.97; P<0.001) between breast height diameter and woody AGB or stem mass (Fig. 2, **IV**), which serves as a good basis for compiling country-specific general downy birch growth models. The average value of stemwood density for downy birch (Table 4, **IV**) found in the present study was lower than the corresponding values reported for silver birch in Estonia (0.65 g cm^{-3}) (Kasesalu 1965).

Although an average C content of 50% in dry mass is normally used to calculate C accumulation in woody biomass, several studies (Laiho and Laine 1997; Bert & Danjon 2006; Zhang *et al.* 2009) have demonstrated that the C content of different tree species and in different woody biomass fractions may vary in a broad range (44%-56%). The weighted average C content in woody biomass found in the present study, at 48%, was slightly lower than that reported in a similar Finnish study at 49.3% (Hytönen & Aro 2012).

Although roots are essential contributors to NPP and play an important role in the C cycling of all forest ecosystems (Prescott *et al.* 2016),

empirical data of the belowground coarse root biomass of birch are rare (Repola 2008; Varik *et al.* 2013; Hunziker *et al.* 2014). Several factors may affect the root-shoot ratio (Cairns *et al.* 1997) and trees growing on peatlands may allocate more biomass to the belowground parts than trees growing on mineral soils (Laiho & Finer 1996). This was also confirmed in our study: the share of the roots (28%) in the middle-aged downy birch stand was higher than the corresponding share (21%) in a silver birch stand of similar age growing on mineral soil (Varik *et al.* 2013).

Above- and belowground litter flux

The annual aboveground litter flux was of the same magnitude in all studied stands, except for the oldest stand, which can be explained by its lower density (Table 1, **IV**). In the studied stands leaf mass stabilized at optimal level already in the 12-year-old stand, i.e. at a quite early stage.

Although fine root (d<2 mm) biomass (FRB) forms a relatively small share in the total biomass of trees (Brunner & Godbold 2007), they contribute significantly to C cycling in forest ecosystems (Gill & Jackson 2000; Finér *et al.* 2011). The contribution of fine roots depends on many factors, among them stand age and soil type (Finér *et al.* 1997; Vanninen & Mäkelä 1999; Ostonen *et al.* 2011). In the present study the FRB of downy birch was of the same magnitude in all stands irrespective of age (Table 7, **IV**). The largest share of FRB was located in the upper 0-10 cm soil layer in all cases, which is a very typical pattern for various forests (Finér *et al.* 2007; Helmisaari *et al.* 2007) owing to the larger nutrient pool in the topsoil (Ostonen *et al.* 2005; Garkoti 2010).

The annual fine root production (FRP) of the studied stands was high (1.8-3 t ha^{-1} yr^{-1}) and did not depend on stand age (Table 7, **IV**). Because of high FRP, average fine root longevity was low and turnover was fast. Turnover rate varied between 1 and 2 yr^{-1}, which was significantly higher than that estimated for silver birch on mineral soils (0.5-0.7 yr^{-1}) (Varik *et al.* 2015). An average fine root turnover rate of 1.0 yr^{-1} for European broad-leaved deciduous trees has been used in biogeochemical models (Brunner *et al.* 2013). However, despite the high turnover rate, the annual C input into soil via fine root litter may have even been underestimated, since we sampled the root meshes once per year, in October, while FRP peaked in summer (Aosaar *et al.* 2013; Rytter 2013; Varik *et al.* 2015).

As discussed above (ch 6.1.), dying and decomposition of fine roots in closed canopy forests are continuous long lasting processes and FRP is a steady state C flux into the soil; such an approach has also been applied in other studies (Meyer *et al.* 2013; Varik *et al.* 2015; Uri *et al.* 2017a).

Carbon output

The estimated annual Rh efflux of the studied stands (4.7-6.2 t C ha^{-1}) was close to the upper limit of the reported values for organic soils, at 1.5-6.7 t C ha^{-1} yr^{-1} (Minkkinen *et al.* 2007; Ojanen *et al.* 2010). A larger flux, at 8.1 t C ha^{-1} yr^{-1}, reported by Meyer *et al.* (2013), was recorded for spruce forest on drained fertile peatland. A large Rh flux from the studied stands was expected since after drainage water level decreases and deeper soil layers become available for aerobic heterotrophic degradation (Berg & McClaugherty 2003; von Arnold *et al.* 2005a). Moreover, birch leaf litter is a readily degradable substrate (Berg & Laskowski 2006) and can considerably contribute to total annual Rh (Janssens *et al.* 2001). Despite the high potential of drained *Histosols* for Rh, the estimated annual Rh flux was of same magnitude as that estimated for forests growing on mineral soils in Estonia (Varik *et al.* 2015; Kukumägi *et al.* 2017; Uri *et al.* 2017a; 2019). This may be the consequence of long lasting drainage; probably decomposition of peat is past its peak and the annual Rh flux is stabilized.

Soil temperature was the main driver for the seasonal dynamics of Rs and Rh (Minkkinen *et al.* 2007; Mäkiranta *et al.* 2008 and 2009) and described 68-92% of the variation in the respiration rates. In the current study, the temperature sensitivity (Q_{10} value) of both of Rs and Rh remained in the range reported for peatlands (2.2-4.9) (Bubier *et al.* 1998; Lafleur *et al.* 2005; Acosta *et al.* 2017). Organic soils have a great potential to lose C with increasing temperature (Kirschbaum 1995; Rustad *et al.* 2001; Wu *et al.* 2011), contributing thereby to the greenhouse effect (Bellamy *et al.* 2005). Thus estimation of Rh and calculation of the Q_{10} values of Rh for peatland soils is especially important (Gorham 1991). For comparison, the Q_{10} values of Rh were lower in silver birch stands on mineral soils in the years with a dry summer (1.9-3.0) (Varik *et al.* 2015).

Carbon budget

The studied downy birch stands growing on drained fertile peat soils acted as C sinks at the young and middle-age stages, reaching an almost steady state in the pre-mature age and acting as a C source at the over-mature stage. The oldest stand turned to a C source due to decreased woody biomass production, the C efflux (Rh) was roughly similar in all studied stands.

The C balance of a forest stand can significantly change with ageing (Kolari *et al.* 2004). Old stands can become weak C sinks or even sources of C (Goulden *et al.* 1996; Lindroth *et al.* 1998) due to decreased biomass production i.e. C emission through soil Rh exceeds the C input. In forests growing on drained organic soils, the high C uptake by trees can often compensate for intensive Rh (Minkkinen *et al.* 2002; Hargreaves *et al.* 2003). Since young downy birch stands act as a C sink owing to the intensive annual biomass production of the trees, management of such peatland forests by using optimal rotation length, is essential in terms of effective C accumulation. The recommended rotation length for downy birch stands is usually 50-60 years (Niemistö *et al.* 2008) and thus a 78-year-old stand is over-mature. The maximum rotation length for downy birch is 70-80 years considering its biological ageing, with decreased growth and an increased risk of rot (Hynynen *et al.* 2010). Further, reforestation of these areas after clear-cut by more productive tree species like black alder (*Alnus glutinosa*) or Norway spruce (*Picea abies*) would be a reasonable option. At same time, despite their high productivity, spruce stands on organic soils may be sensitive to wind throw.

The organic C input to the soil from above- and belowground litter in all stands accounted for 36-56% of NPP. The contribution of the understorey vegetation to NPP was modest and decreased in the older stands. The annual Rh flux exceeded the organic C input into the soil (litter) in all studied stands (Table 9, **IV**), which indicated soil C loss.

Moreover, to estimate the total effect of drainage on the atmosphere and climate change, the emissions of other GHG should be taken into account because they may change balances in terms of potential of global warming. In the present study, methane (CH_4) and N_2O emissions from the soil were not measured. We assume that methane emission

was modest, as it is usually decreased in drained soils (von Arnold *et al.* 2005ab; Ilomets 1996; Martikainen *et al.* 1993; Salm *et al.* 2009). According to Meyer *et al.* (2013), CH_4 emission was very low and negative in a fertile drained organic soil under a Norway spruce stand in all cases. However, fluctuations in groundwater level may significantly increase CH_4 emission (Mander *et al.* 2015).

The more powerful greenhouse gas (N_2O) emission may be also appreciable since drained *Histosols* have large nitrogen N content (Lõhmus 1984). Still, studies in forested drained peatlands demonstrated a modest source of N_2O (Ojanen *et al.* 2010; Lohila *et al.* 2011). Regarding the other GHG, more detailed further studies are needed.

6.4. Annual net nitrogen mineralization in a well-drained downy birch forest ecosystem

Soil mineral nitrogen dynamics

A large soil N pool is typical of drained eutrophic swamp forests (Westman & Laiho 2003). In this study the total soil N pool in the 0-10 cm upper soil layer in the studied stand was about 5 t N ha^{-1} and even amounted to 20 t N ha^{-1} in the soil layer up to 40 cm (Table 2, **II**). This exceeds greatly the N storages reported for mineral soils of the boreal and hemiboreal forest ecosystems (Gundersen 1995), including Estonian forests (Uri *et al.* 2003, 2008; Becker *et al.* 2015, 2016). The large total soil N storage in organic soils can be explained by the presence of a deep peat layer and the high N content of well decomposed peat. However, a large soil N pool does not reflect the amount of N actually available for uptake by plants. Helmisaari (1995) reports that typically only about 0.1-1 % of the soil N pool in boreal forests is available for plants in the form of inorganic N. The corresponding share of 1-3.5 % in the upper soil N pool has been found to be available as mineral N (Baldock & Nelson 2000; Uri *et al.* 2008; Becker *et al.* 2015). In this study the share of mineral N in the total N pool (2.4 %) in the upper 0-10 cm soil layer was in a similar range.

The annual dynamics of soil mineral N of the studied birch stand demonstrated soil mineral N content peaking in August and November. The increase of soil mineral N content in autumn is a quite typical pattern which can be mainly explained by ceased N uptake by plants and by the

input of fresh organic matter through litter (Uri *et al.* 2003, 2008; Becker *et al.* 2015). Soil mineral N content was low in spring and increased until autumn, which is in accordance with the dynamics of NNM intensity. High soil mineral N content during the vegetation period (Fig. 2, **II**) is the result of favourable conditions promoting NNM.

Annual net nitrogen mineralization

Nitrogen net mineralization (NNM) was estimated for the upper 0-10 cm soil layer, where nutrient content and microbial biomass and activity are higher and fine root biomass is the largest (Lõhmus *et al.* 2006; Uri *et al.* 2009; Aosaar *et al.* 2013; Varik *et al.* 2013). Most of annual mineral N is formed in the uppermost soil layer; According to Persson & Wirén (1995), an average of 78% of NNM occurs in the 0-10 cm topsoil layer and the remaining 22% in the 10-50 cm layer of mineral soil. Connell *et al.* (1995) concluded that 75-85% of NNM generally occurs in the upper 0-20 cm soil layer. This has also been confirmed in Estonian studies (Uri *et al.* 2003, 2008; Becker *et al.* 2016).

It has been reported that soil nitrate N content is mainly affected by temperature and drainage, but soil ammonium N content depends largely on soil moisture (Glina *et al.* 2016). However, in the current study we did not find any positive correlation between NH_4^+-N and soil moisture content. It confirmed that NNM is mainly affected by soil temperature and pH (Tietema & Verstraten 1992) while the effect of soil moisture is not very clear (Uri *et al.* 2008; Becker *et al.* 2015; 2016). The effect of soil temperature on NNM intensity was evident also in the present study, while the effects of pH and soil moisture content were not found. Nitrification was the major process of N transformation in the studied stand accounting for 100% of total annual NNM (Table 3, **II**). The favourable range for nitrification is pH 3.9 to 6.3 (Van Praag & Weissen 1973); low pH often restricts nitrification and almost no nitrification can be detected at pH<4 (Persson & Wiren 1995). Since the study site soil, *Drainic Eutric Histosol,* can be characterized as fertile and nutrient rich and thus pH is relatively high, nitrification was a favoured process. In the present study the soil C:N ratio for the upper 0-10 cm layer in the birch stands was 15.3 (Table 2, **II**), which is of the same magnitude as that for fertile forest site types on mineral soils (Cools *et al.* 2014, Uri *et al.* 2014, 2015; Varik *et al.* 2015; Becker *et al.* 2015, 2016).

Annual NNM in the birch stand was estimated roughly at 130 kg N ha^{-1} yr^{-1}. According to literature data (Aber *et al.* 1989; Scott & Binkley 1997; Magill *et al.* 2000; Uri *et al.* 2011; Becker *et al.* 2015), the annual NNM in deciduous stands varies between 24 kg ha^{-1} yr^{-1} and 200 kg ha^{-1} yr^{-1} and can usually cover a major part of the annual N demand of these stands.

Soil N dynamics is strongly related to carbon cycle (C). The studied downy birch stand was highly productive and acted as a C sink (Uri *et al.* 2017a). In forests growing on drained organic soils, the high C uptake of trees can often compensate for intensive soil respiration (Minkkinen *et al.* 2002; Hargreaves *et al.* 2003) and from the point of view of productivity and more effective C sequestration, available soil N is a crucial factor. Stand productivity depends on the co-effect of many different factors, among them high annual NNM intensity, which ensure vigorous growth of trees and high C accumulation. As a result of the long term drainage of swamps, there has emerged a fertile specific site type with high production capacity, which is very favourable in terms of forest management.

6.4. The effect of harvesting thinning on NNM and leaching in a silver birch stand growing on mineral soil

In the studied silver birch stand the total soil N pool in the upper 10 cm layer was similar both in the control and in the thinned plot (roughly 1.4 t N ha^{-1}) (Table 2, **V**). The total N pool in the 0-30 cm soil layer varied between 3.5 and 3.8 t N ha^{-1}, which remains in the range of the total N pool for boreal forest ecosystems and was, as a rule 1–8 t ha^{-1}, as pointed out above (ch 6.3). In the current study the share of mineral N was higher, accounting for 2.2–3.7% of the soil N pool in the upper 0–10 cm soil over the longer study period (2004-2017). The dynamics of soil mineral N content was affected by thinning: in the thinned plot mineral N fluctuated monthly during the first post-thinning year while in the control plot its content demonstrated a relatively smooth course (Fig. 1, **V**). The lowest mineral N content was recorded in late autumn for both study plots, which can be explained by low soil temperature and decreased NNM.

Mineral soil N content decreased in the course of stand development: when in the same stand (8-year–old) the estimated nitrate N content in 10 cm topsoil varied between 24 and 35 mg kg^{-1} (Uri *et al.* 2008),

then in 2016-2017 it was only 1.7-5.7 mg kg^{-1}. The lower soil mineral N content can be attributed to decreased net nitrification intensity (Table 3, **V**) whose value was roughly threefold lower compared with that for the 8-year-old stand (2004). Of course, the content of mineral N depended on NNM intensity, on the one hand, and on the uptake by plants, on the other hand. In a 10-year-old birch stand the total annual N demand of plants was 118 kg ha^{-1} yr^{-1} (Aosaar *et al.* 2016) and the largest share of annual N demand (60%) was expended for the production of leaves. The foliage mass in broadleaved stands usually reaches a stable level (3-4 t ha^{-1}) at the age of 10 years. Thus we can assume that the magnitude of the annual N demand of plants did not change and the decrease of mineral N in the studied stand was mainly induced by the reduced annual NNM flux.

The dynamics of annual NNM followed a quite characteristic trend, i.e. NNM was more intensive in spring or early summer and in autumn (Fig. 3, **V**), which can be mainly explained by the input of decomposable fresh organic matter to the soil via litter. According to Nadelhoffer *et al.* (1984), mineralization intensity is the highest in spring or early summer (May, June) while another peak occurs at the end of the vegetation period (August, September). Two peaks of annual NNM were also found for grey alder stands of the same age, growing on similar soils on abandoned agricultural land in Estonia: a spring peak in May and a less pronounced autumn maximum in September (Uri *et al.* 2003).

Thinning significantly intensified net nitrification whereas ammonification remained at the same level during the first post-thinning year; the annual cumulative NNM flux was roughly two times as high in the thinned plot as in the control plot, 30 and 54 kg ha^{-1} yr^{-1}, respectively (Table 3, **V**). In the second year after thinning this difference was levelled out (Fig. 3, **V**), and although NNM in the thinned plot was higher in almost all study periods, a statistically significant difference was only found for one study month (July-August). Thus, the effect of thinning on NNM intensity was of short duration, being limited to one post-thinning year.

Owing to the fact that the silver birch stand had a long study history (Uri *et al.* 2007, 2008), the decrease of annual NNM became apparent. In the 8-9 year-old stand (2004-2005) the annual NNM flux was roughly 100 kg N ha^{-1} yr^{-1} estimated for the upper 10 cm soil layer (Table 3, **V**). Ten years later (2014-2015) it was almost two times as low (roughly 50 kg N ha^{-1}

yr^{-1}) and in the 21-year-old stand it was only 30 kg N ha^{-1} yr^{-1} (Table 3, **V**). This probably indicates a weakening of the effect of land use history: a birch stand had emerged on former agricultural land. The more intensive NNM in this stand, compared with the adjacent non-forested grassland, was induced by the trees in an earlier developmental phase (Uri *et al.* 2008). Thereafter annual NNM started to decrease; however, it was nitrification intensity that decreased while the rate of ammonification remained almost the same. Some studies support the standpoint that potential N mineralization and nitrification in forested old fields are the highest in the early forest succession period (Thorne & Hamburg 1985). Some researchers found an increase in NNM, especially nitrification, with increasing stand age (Zak *et al.* 1990; Robertson & Vitousek 1981). Also the share of nitrification in total NNM varied during stand development: when in the 8-year-old stand (2004) nitrification made up ca 60% of total NNM, then ten years later it made up more than 70% and in the 21-year old stand it had decreased to around 50%. Thinning affected this share, in our study it was around 70% of total soil NNM (Table 3, **V**).

Leaching of N in the silver birch stand was modest. In the control plot it was even larger (5.5 kg N ha^{-1} yr^{-1}) than estimated for the 10-year-old stand (ca 1 kg N ha^{-1} yr^{-1}) (Aosaar *et al.* 2016). N leaching may vary to a large extent for different years, depending mostly on annual precipitation as well as on N transformation processes in soil. The effect of thinning on annual N leaching was contrary to our expectations. Usually, thinning should increase both the amount of percolated water and nutrient release, as a consequence of decreased canopy closure and increased precipitation onto forest ground, as well as a consequence of the additional input of organic matter to soil from fine root necromass and residues. In this study, annual N leaching in the thinned plot was smaller due to a lesser amount of percolated water. The only rational explanation for this phenomenon would be more intensive growth of the herbaceous understorey in the thinned area. Because of favourable light conditions in the thinned plot, the growth of the herbaceous understorey intensified greatly, which prevented precipitation reaching the soil and contributed to the quicker uptake of water by plants.

7. CONCLUSIONS

1. In terms of organic litter decomposition, the results appeared to be in contradiction to the proposed hypothesis: the decomposition dynamics of grey alder and silver birch leaves and roots was not significantly different in similar soils. For both species, the decomposition of the coarser root fraction (2<d<5mm) was faster than the decomposition of the fine roots (d<2mm). In both grey alder and silver birch stands, the annual input of nitrogen to soil from decomposed leaf litter was several times higher than from root litter.

2. The stated hypothesis was proved, the young and middle-aged downy birch stands growing on drained fertile *Histosols* acted as effective C sinks. Thus at least young and middle-age drained downy birch forest acts as a C sink, i.e. more intensive C accumulation through increased biomass production exceeds intensified Rh. In the 38-year-old stand C output and input fluxes were in balance, such a stand was C neutral. However, the over-matured downy birch stand was a C emitting ecosystem, i.e. a C source.

The annual Rh flux was of same magnitude in the studied stands and did not depend on stand age or depth of the peat layer. The annual organic C input into the soil (above- and belowground litter, understorey vegetation) was smaller than the annual Rh flux irrespective of stand age, indicating continuous mineralization of peat and a decrease of the soil C pool.

The ecosystem C cycle was strongly related to soil nitrogen (N) dynamics; for more effective C sequestration, available soil N is crucial. In the studied middle-aged downy birch stand, annual net nitrogen mineralization (NNM) was intensive, ensuring a considerable amount of available N for plant uptake and hence effective C accumulation.

3. The stated hypothesis was proved partly; the oldest grey alder stand was indeed a weak C source. However, also young stands in post clear-cut areas may act as C sources at an earlier stage of development due to the decomposing organic matter from the previous forest generation, i.e. previous land use plays a crucial role in this respect. Generally, grey alder stands are C accumulating ecosystems, although the annual production

of stands may be highly variable, depending on weather conditions during the growing period rather than on stand age.

The repeated time-series measurement method yields more reliable estimation of C accumulation in forest ecosystems and demonstrated a strong effect of the year, i.e. weather conditions. The results of the present study support our earlier finding that soil C exchange may depend on land use history; intensive C accumulation in soil took place in a stand growing on former agricultural land. Grey alder stands on forest land accumulated C mainly in biomass, while in first generation stands (growing on previously non-forested land) C was accumulated both in soil and biomass.

4. In the silver birch stand, thinning increased the annual NNM flux through increased nitrification, which confirmed stated hypotheses However, this effect was of short term and was only revealed for the first post-thinning year and disappeared thereafter. The long-term dynamics of annual NNM in the silver birch stand demonstrated a significant decrease, which may indicate the declining effect of land use history.

However, annual N leaching in the studied birch stand was generally small and thinning did not induce more intensive N leaching. Moreover, in the thinned birch stand N leaching was even smaller compared with the control plot.

Suggestions for practical forestry

The present thesis provided more basic knowledge in two studies (**I**, **II**) dealing with soil processes that are crucial for nutrient cycling in forest ecosystems: organic litter decomposition and annual net nitrogen mineralization. Some conclusions of three (**III**; **IV**; **V**) studies addressed quite directly forest managers, decision makers and politicians.

Since grey alder stands have a great potential as sources of C neutral biomass in the nearest future, all potential environmental effects related to the management of grey alder stands should be studied. It was found that grey alder stands can be described as effective C accumulating ecosystems and more extensive management of such stands does not involve environmental risks in terms of C cycling. Since the dynamics of C accumulation in the biomass of trees depended on stand age, optimal

rotation length for the management of such stands is essential from the point of view of effective C sinks.

Since young and middle-aged downy birch stands on drained fertile *Histosols* acted as effective C sinks while the eldest stand was a C emitting system, then for more effective C accumulation, optimization of rotation length in the management of downy birch stands on drained swamps may be an essential issue.

Moreover, in order to increase the C sequestration ability of stands, also the tree species is of importance. Further, reforestation of areas after clear-cut by more productive tree species like black alder (*Alnus glutinosa*) or Norway spruce (*Picea abies*) would be a reasonable option. However, despite their high productivity, spruce stands on organic soils may be sensitive to wind throw.

Thinning affected the nitrogen mineralization process, thereby introducing more of available N for production of trees, which can be a positive outcome of harvesting thinning. At the same time, higher soil N content did not induce N leaching in the thinned stand. Harvesting thinning in the young silver birch stand increased available soil N but did not increase N loss from the ecosystem. Thus we can conclude that harvesting thinning in silver birch stands growing at a fertile site do not involve environmental risks in terms of N losses.

REFERENCES

Aber, J.D., Melillo, J.M. 1982. Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. Can. J. Bot. 60, 2263–2269.

Aber, J.D., Nadelhoffer, J.K., Steudler, P., Melillo, J.M. 1989. Nitrogen saturation in Northern forest ecosystems. Bioscience. 39(6), 378–386.

Acosta, M., Juszczak, R., Chojnicki, B., Pavelka, M., Havránková, K., Lesny, J., et al. 2017. CO2 fluxes from different vegetation communities on a peatland ecosystem. Wetlands. 37(3), 423–435.

Adams, M.A., Polglase, P.J., Attiwill, M.P., Weston, C.J. 1989. In situ studies on nitrogen mineralization and uptake in forest soils: some comments on methodology. Soil Biol. Biochem. 21(39), 423–429.

Andersson, P., Berggren, D., Nilsson, I. 2002. Indices for nitrogen status and nitrate leaching from Norway spruce (*Picea abies* (L.) Karst.) stands in Sweden. Forest Ecol. Manag. 157(1–3), 39–53.

Aosaar, J., Mander, Ü., Varik, M., Becker, H., Morozov, G., Maddison, M., Uri, V. 2016. Biomass production and nitrogen balance of naturally afforested silver birch (*Betula pendula* Roth.) stand in Estonia. Silva Fenn. 50(4), 1–19.

Aosaar, J., Varik, M., Lõhmus, K., Ostonen, I., Becker, H., Uri, V. 2013. Long-term study of above- and below-ground biomass production in relation to nitrogen and carbon accumulation dynamics in a grey alder (*Alnus incana* (L.) Moench) plantation on former agricultural land. Eur. J. For. Res. 132(5–6), 737–749.

Bahn, M., Reichstein, M., Davidson, E.A., Grünzweig, J., Jung, M., Carbone, M.S., Epron, D., Misson, L., Nouvellon, Y., Roupsard, O., Savage, K., Trumbore, S.E., Gimeno, C., Curiel Yuste, J., Tang, J., Vargas, R., Janssens, I.A. 2010. Soil respiration at mean annual temperature predicts annual total across vegetation types and biomes. Biogeosciences. 7, 2147–2157.

Baldocchi, D. 2014. Measuring fluxes of trace gases and energy between ecosystems and the atmosphere – the state and future of the eddy covariance method. Glob. Change Biol. 20, 3600–3609.

Baldock, J.A., Nelson, P.N. 2000. Soil organic matter. In: Sumner, M.E. (Ed.). Handbook of Soil Science. CRC Press, Boca Raton, USA.

Bardulis, A., Lazdina, D., Daugaviete, M., Bardule, A., Daugavietis, U., Rozitis, G., 2015. Above ground and below ground biomass in grey alder *Alnus incana* (L.) Moench. young stands on agricultural land in central part of Latvia. Agron. Res. 13(2), 277–286.

Becker, H., Aosaar, J., Varik, M., Morozov, G., Aun, K., Mander, Ü., Soosaar, K., Uri, V. 2018. Annual net nitrogen mineralization and litter flux in well-drained downy birch, Norway spruce and Scots pine forest ecosystems. Silva Fenn. 52(4), 1-18.

Becker, H., Aosaar, J., Varik, M., Morozov, G., Kanal, A., Uri, V. 2016. The effect of Norway spruce stump harvesting on net nitrogen mineralization and nutrient leaching. Forest Ecol. Manag. 377, 150–160.

Becker, H., Uri, V., Aosaar, J., Varik, M., Mander, Ü., Soosaar, K., Hansen, R., Teemusk, A., Morozov, G., Kutti, S., Lõhmus, K. 2015. The effects of clear-cut on net nitrogen mineralization and nitrogen losses in a grey alder stand. Ecol. Eng. 85, 237–246.

Bellamy, P.H., Loveland, P.J., Bradley, R.I., Lark, R.M., Kirk, G.J. 2005. Carbon losses from all soils across England and Wales 1978–2003. Nature 437, 245–248.

Berg, B. 1984. Decomposition of root litter and some factors regulating the process: long-term root litter decomposition in a Scots pine forest. Soil Biol. Biochem. 16, 609–617.

Berg, B. 1986. Nutrient release from litter and humus in coniferous forest soils – a mini-review. Scand. J. Forest Res. 1, 350–369.

Berg, B. 1988. Dynamics of nitrogen (15N) in decomposing Scots pine (Pinus sylvestris) needle litter. Long-term decomposition in a Scots pine forest VI. Can J. Bot. 66, 1539–1546.

Berg, B. 2000. Litter decomposition and organic matter turnover in north- ern forest soils. Forest Ecol. Manag. 133(1–2), 13–22.

Berg, B., Ekbohm, G., McClaugherty, C. 1984. Lignin and holocellulose relations during long-term decomposition of some forest litters. Long-term decomposition in a Scots pine forest. IV. Can. J. Botany. 62, 2540–2557.

Berg, B., Laskowski, R. 2006. Litter decomposition: a guide to carbon and nutrient turnover, in: Litter Decomposition: a Guide to Carbon and Nutrient Turnover, 1st Edition Advances in ecological research 38. Elsevier Academic Press, UK.

Berg, B., McClaugherty, C. 2003. Plant Litter. Decomposition, Humus Formation, Carbon Sequestration. Springer, Berlin Heidelberg New York.

Berg, B., Staaf, H. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. Ecol. Bull. 33, 163–178.

Berg, B., Staaf, H., Wesser, B. 1987. Decomposition and nutrient release in needle litter from nitrogen-fertilized Scots pine (*Pinus sylvestris*) stands. Scand. J. Forest Res. 2, 399–415.

Berg, B., Wessen, B., Ekbohm, G. 1982. Nitrogen level and lignin decomposition in Scots pine needle litter. Oikos. 38, 291–296.

Bert, D., Danjon, F. 2006. Carbon concentration variations in the roots, stem and crown of mature Pinus pinaster (Aait.). Forest Ecol. Manag. 222, 279–295.

Binkley, D. 2005. How nitrogen fixing trees change soil carbon. In: Binkley, D., Menyailo, O. (Eds.) Tree Species Effects on Soils: Implications for Global Change. NATO Sciences Series, Kluwer Academic Publishers, Dordrecht.

Bocock, K.L. 1963. The digestion and assimilation of food by Glomeris marginata. In: Doeksen, J., Van der Drift, J., (eds). Soil organisms. Amsterdam: North Holland Publishing, p. 85–91.

Brunner, I., Bakker, M.R., Björk, R.G., Hirano, Y., Lukac, M., Aranda, X., et al. 2013. Fine-root turnover rates of European forests revisited: an analysis of data from sequential coring and ingrowth cores. Plant Soil. 362, 357–372.

Brunner, I., Godbold, D.L. 2007. Tree roots in a changing world. J. For. Res. – Jpn. 12, 78–82.

Bubier, J.L., Crill, P.M., Moore, T.R., Savage, K., Varner, R.K. 1998. Seasonal patterns and controls on net ecosystem CO2 exchange in a boreal peatland complex. Global Biogeochem. Cycles. 12, 703–714.

Cairns, M., Brown, S., Helmer, E., Baumgardner, M. 1997. Root biomass allocation in the world's upland forests. Oecologia. 111, 1–11.

Cannell, M.G.R. 1999. Growing trees to sequester carbon in the UK: answers to some common questions. Forestry. 72(3), 237–247.

Chamier, A.C. 1987. Effect of pH on microbial degradation of leaf litter in seven streams of the English Lake District. Oecologia. 71, 491–500.

Chapin, F.S., Woodwell, G.M., Randerson, J.T., Rastetter, E.B., Lovett, G.M., Baldocchi, D.D., et al. 2006. Reconciling carbon-cycle concepts, terminology, and methods. Ecosystems. 9(7), 1041–1050.

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J. 2001. Net primary production in forests: concepts and field methods. Ecol. Appl. 11(2), 356–370.

Connell, M.R., Raison, R.J., Khanna, P.K. 1995. Nitrogen mineralization in relation to site history and soil properties in a range of Australian forest soils. Biol. Fert. Soils. 20(4), 213–220.

Cools, N., Vesterdal, L., De Vos, B., Vanguelova, E., Hansen, K. 2014. Tree species is the major factor explaining C:N ratios in European forest soils. Forest Ecol. Manag. 311, 3–16.

Coûteaux, M.M., Bottner, P., Berg, B. 1995. Litter decomposition, climate and litter quality. Trends Ecol Evol. 10(2), 63–66.

Dilly, O., Munch, J.C. 1996. Microbial biomass content, basal respiration and enzyme activities during the course of decomposition of leaf litter in a black alder (*Alnus glutinosa* (L.) Gaertn.) forest. Soil Biol. Biochem. 28, 1073–1081.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Texler, M.C., Wisniewski, J. 1994. Carbon pools and fluxes of global forest ecosystems. Science. 263, 185–190.

Duran, J., Morse, J.L., Groffman, P.M. 2012. Comparison of in situ methods to measure N mineralization rates in forest soils. Soil Biol. Biochem. 46, 145–147.

Edmonds, R.L. 1984. Long-term decomposition and nutrient dynamics in Pacific silver fir needles in western Washington. Can. J. For. Res. 14, 395–400.

Edmonds, R.L., Thomas, T.B. 1995. Decomposition and nutrient release from green needles of western hemlock and Pacific silver fir in an old-growth temperate rain forest, Olympic National Park, Washington. Can. J. For. Res. 25(7), 1049–1057.

Edwards, C.A., Bohlen, P.J. 1996. Biology and ecology of earthworms. 3rd ed. London: Chapman & Hall.

Eissenstat, D., Yanai, R.D. 1997. The ecology of root lifespan. Adv. Ecol. Res. 27, 1–60.

Eno C.F. 1960. Nitrate production in the field by incubating the soil in polyethylenebags. In: Proceedings of the Soil Science Society of America 24(4), 277–279.

Epron, D. 2009. Separating autotrophic and heterotrophic components of soil respiration: lessons learned from trenching and related root-exclusion experiments. In: Kutsch, W.L., Bahn, M., Heinemeyer, A. (eds). Soil carbon dynamics: an integrated methodology. Cambridge University Press, UK, pp. 157–168.

Fan, P., Guo, D. 2010. Slow decomposition of lower order roots: a key mechanism of root carbon and nutrient retention in the soil. Oecologia. 163, 509–515.

Fang, J.Y., Liu, G.H., Zhu, B., Wang, X.K., Liu, S.H., 2007. Carbon budgets of three temperate forest ecosystems in Dongling Mt. Beijing, China. Sci. China Ser. D: Earth Sci. 50(1), 92–101.

Fang, S., Lin, D., Tian, Y., Hong, S. 2016. Thinning Intensity Affects Soil-Atmosphere Fluxes of Greenhouse Gases and Soil Nitrogen Mineralization in a Lowland Poplar Plantation. Forests. 7(141), 1–16.

Feng, Z., Rütting, T., Pleijel, H., Wallin, G., Reich, P. B., Kammann, C.I., Newton, P.C.D., Kobayashi, K., Luo, Y., Uddling, J. 2015. Constraints to nitrogen acquisition of terrestrial plants under elevated CO_2. Glob. Change Biol. 21(8), 3152–3168.

Finér, L., Helmisaari, H.-S., Lõhmus, K., Majdi, H., Brunner, I., Børja, I., Eldhuset, E., Godbold, D., et al. 2007. Variation in fine root biomass of three European tree species: Beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.). Plant Biosyst. 141, 394–405.

Finér, L., Messier, C., Granpré, L. 1997. Fine-root dynamics in mixed boreal conifer – broadleafed forest stands at different successional stages after fire. Can. J. Forest Res. 27, 304–314.

Finér, L., Ohashi, M., Noguchi, K., Hirano, Y. 2011. Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. Forest Ecol. Manag. 262(11), 2008–2023.

Garkoti, S.C. 2010. Fine root dynamics in three central Himalayan high elevation forests ranging from closed canopied to open-canopied treeline vegetation. J. For. Res-Jpn. 16(2), 136-143.

Gaumont-Guay, D., Black, T.A., Barr, A.G., Griffis, T.J., Jassal, R.S., Krishnan, P., Grant, N., Nesic, Z. 2014. Eight years of forestfloor CO2 exchange in a boreal black spruce forest: spatial integration and long-term temporal trends. Agric For. Meteorol. 184, 25–35.

Gill, R.A., Jackson, R.B. 2000. Global patterns of root turnover for terrestrial ecosystems. New Phytol. 147, 13–31.

Glina B., Bogacz A., Woźniczka P. 2016. Nitrogen mineralization in forestry-drained peatland soils in the Stołowe Mountains National Park (Central Sudetes Mts). Soil Sci. 67(2), 64–72.

Goebel, M., Hobbie, S.E., Bulaj, B., Zadworny, M., Archibald, D.D., Oleksyn, J., Reich, P.B., Eissenstat, D.M. 2011. Decomposition of the finest root branching orders: linking belowground dynamics to fine-root function and structure. Ecol. Monogr. 81, 89–102.

Goodale, C.L., Aber, J.D. 2001. The long term effects of land-use history on nitrogen cycling in northern hardwood forests. Ecol. Appl. 11(1), 253–267.

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol. Appl. 1, 182–195.

Gosz, J.R., Likens, G.E., Bormann, F.H. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. Ecol. Monog. 43, 173–191.

Gough, C.M., Vogel, C.S., Schmid, H.P., Curtis, P.S. 2008. Controls on annual forest carbon storage: Lessons from the past and predictions for the future. Bioscience. 58, 609–622.

Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C, Wofsy, S.C. 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. Glob. Change Biol. 2, 159–168.

Granhall, U. 1994. Biological fertilization. Biomass Bioenerg. 6, 81–91.

Granhall, U., Verwijst, T. 1994. Grey alder (*Alnus incana*) a N2-fixing tree suitable for energy forestry. In: Hall, D.O., Grassi, G., Scheer, H. (eds). Biomass for energy and industry. Ponte Press, Bochum, pp 409–413.

Gundersen P. 1995. Impacts of nitrogen deposition: scientific background. In: Forsius, M., Kleemola, S. (eds.). Fourth Annual Synoptic Report, Helsinki. p. 9–18.

Hanselman, T.A., Graetz, D.A., Obreza, T.A. 2004. A comparison of in situ methods for measuring net nitrogen mineralization rates of organic soil amendments. J. Environ. Quality. 33, 1098–1105.

Hargreaves, K.J., Milne, R., Cannell, M.G.R. 2003. Carbon balance of afforested peatland in Scotland. Forestry. 76(3), 299–317.

Harmon, M.E., Bond-Lamberty, B., Tang, J., Vargas, R., 2011. Heterotrophic respiration in disturbed forests: A review with examples from North America. J. Geophys. Res. 116, G00K04.

Hart, S.C., Stark, J.M., Davidson, E.A., Firestone, M.K. 1994. Nitrogen mineralization, immobilization and nitrification. Methods of soil analyses. Part 2. Microbial and biochemical properties. SSSA Book Series 5, USA, pp. 985–1018.

Hartmann, J., West, A.J., Renforth, P., Köhler, P., De La Rocha, C.L., Wolf-Gladrow, D.A., Dürr, H.H., Scheffran, J. 2013. Enhanced chemical weathering as a geoengineering strategy to reduce atmospheric carbon dioxide, supply nutrients, and mitigate ocean acidification. Rev. Geophys. 51(2), 113–149.

Helmisaari H.-S. 1995. Nutrient cycling in *Pinus sylvestris* stand in eastern Finland. Plant Soil. 168(1), 327–336.

Helmisaari, H.-S., Derome, J., Nöjd, P., Kukkola, M. 2007. Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. Tree Physiol. 27, 1493–1504.

Hirano, Y., Noguchi, K., Ohashi, M., Hishi, T., Makita, N., Fujii, S., Finér, L. 2009. A new method for placing and lifting root meshes for estimating fine root production in forest ecosystems. Plant Root. 3, 26–31.

Horodecki, P., Jagodziński, A.M. 2017. Tree species effects on litter decomposition in pure stands on afforested post-mining sites. Forest Ecol. Manag. 406, 1–11.

Hunziker, M., Sigurdsson, B.D., Halldorsson, G., Schwanghart, W., Kuhn, N. 2014. Biomass allometries and coarse root biomass distribution of mountain birch in southern Iceland. Icel. Agric. Sci. 27, 111–125.

Hynynen, J., Niemistö, P., Viherä-Aarnio, A., Brunner, A., Hein, S., Velling, P. 2010. Silviculture of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) in northern Europe. Forestry. 83(1), 103–119.

Hytönen, J., Aro, L. 2012. Biomass and nutrition of naturally regenerated and coppiced birch on cutaway peatland during 37 years. Silva Fenn. 46(3), 377–394.

Hytönen, J., Saarsalmi, A. 2015. Biomass production of coppiced grey alder and the effect of fertilization. Silva Fenn. 49(1), 1–16.

Hyvönen, R., Persson, T., Andersson, S., Olsson, B., Ågren, G.I., Linder, S., 2007. Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. Biogeochemistry. 89, 121–137.

Ilomets, M. 1996. Temporal changes of Estonian peatlands and carbon balance. In: Punning, J.M. (Ed.), Estonia in the System of Global Climate Change. Institute of Ecology, Tallinn, Estonia, pp. 65–75.

IUSS Working Group WRB, 2006. World Reference Base for soil resources 2006. In: World Soil Resources Reports No 103, second ed. FAO, Rome.

Kasesalu, A. 1965. Kasepuidu füüsikalis-mehaanilistest omadustest erinevates kasvukohatüüpides (The physical and mechanical qualities of silver birch timber growing in different site types). Metsanduslikud Uurimused. 4, 149–157 (in Estonian).

Kataja-aho, S., Samolander, A., Fritze, H., Norrgård, S., Haimi, J. 2012. Responses of soil carbon and nitrogen to stump removal. Silva Fenn. 46(2), 169–179.

Keith, H., Mackey, B.G., Lindenmayer, D.B. 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. P. Natl. Acad. Sci. USA. 106, 11635–11640.

Kirschbaum, M.U.F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biol. Biochem. 27, 753–760.

Knohl, A., Soe, A.R.B., Kutsch, W.L., Göckede, M., Buchmann, N. 2008. Representative estimates of soil and ecosystem respiration in an old beech forest. Plant Soil. 302, 189–202.

Kolari, P., Hari, P., Berninger, F., Pumpanen, J., Rannik, Ü., Ilvesniemi, H. 2004. Carbon balance of different aged Scots pine forests in Southern Finland. Glob. Change Biol. 10, 1106–1119.

Körner, C. 2017. A matter of tree longevity. Science. 355, 130–131.

Kriiska, K., Frey, J., Asi, E., Kabral, N., Uri, V., Aosaar, J., Varik, M., Napa, Ü., Apuhtin, V., Timmusk, T., Ostonen, I. 2019. Variation in

annual carbon fluxes affecting the SOC pool in hemiboreal coniferous forests in Estonia. Forest Ecol. Manag. 433, 419−430.

Kukumägi, M., Ostonen, I., Uri, V., Helmisaari, H.-S. Kanal, A., Kull, O., Lõhmus, K. 2016. Variation of soil respiration and its components in hemiboreal Norway spruce stands of different ages. Plant Soil. 414(1), 265–280.

Kukumägi, M., Ostonen, I., Uri, V., Helmisaari, H.-S., Kanal, A., Kull, O., Lõhmus, K. 2017. Variation of soil respiration and its components in hemiboreal Norway spruce stands of different ages. Plant Soil. 414(1), 265–280.

Kuzyakov, Y. 2006. Sources of CO2 Efflux from Soil and Review of Partitioning Methods. Soil Biol. Biochem. 38(3), 425-448.

Lafleur, P.M., Moore, T.R., Roulet, N.T., Frolking, S. 2005. Ecosystem respiration in a cool temperate bog depends on peat temperature but not water table. Ecosystems. 8, 619–629.

Laiho, R., Finér, L. 1996. Changes in root biomass after water- level drawdown on pine mires in southern Finland. Scand. J. Forest Res. 11, 251–260.

Laiho, R., Laine, J. 1997. Tree stand biomass and carbon content in an age sequence of drained pine mires in southern Finland. Forest Ecol. Manag. 93, 161–169.

Law, B.E., Sun, O.J., Campbell, J., Van Tuyl, S., Thornton, P.E. 2003. Changes in carbon storage and fluxes in a chronosequnece of ponderosa pine. Glob. Change Biol. 9, 510–524.

Lecerf, A. 2017. Methods for estimating the effect of litterbag mesh size on decomposition. Ecol Model. 362, 65–68.

Lee, K.-H., Jose, S. 2003. Soil respiration, fine root production, and microbial biomass in cottonwood and loblolly pine plantations along a nitrogen fertilization gradient. Forest Ecol. Manag. 185, 263–273.

Leppälammi-Kujansuu, J., Aro, L., Salemaa, M., Hansson, K., Kleja, D.B, Helmisaari, H.-S. 2014. Fine root longevity and carbon input into soil from below- and aboveground litter in climatically contrasting forests. Forest Eco. Manag. 326, 79–90.

Leppelt, T., Dechow, R., Gebbert, S., Freibauer, A., Lohila, A., Augustin, J., et al. 2014. Nitrous oxide emission budgets and land-use-driven hotspots for organic soils in Europe. Biogeosciences. 11, 6595–6612.

Lindroth, A., Grelle, A., Moren, A.S. 1998. Long-term measurements of boreal forest carbon exchange reveal large temperature sensitivity. Glob. Change Biol. 4, 443–450.

Liski, J., Nissinen, A., Erhard, M., Taskinen, O. 2003. Climatic effects on litter decomposition from arctic tundra to tropical rainforest. Glob. Change Biol. 9, 575–584.

Liski, J., Perruchoud, D., and Karjalainen, T. 2002. Increasing Carbon Stocks in the Forest Soils of Western Europe. Forest Ecol. Manag. 169, 163–179.

Lohila, A., Minkkinen, K., Aurela, M., Tuovinen, J.P., Penttilä, T., Ojanen, P., et al. 2011. Greenhouse gas flux measurements in a forestry-drained peatland indicate a large carbon sink. Biogeosciences. 8, 3203–3218.

Lõhmus, E. 1984. Eesti metsakasvukohatüübid. Tallinn, p 76 (In Estonian).

Lõhmus, K., Ivask, M. 1995. Decomposition and nutrient dynamics of fine roots of Norway spruce (*Picea abies* (L.) Karst.) at different sites. Plant Soil. 168/169, 89–94.

Lõhmus, K., Kuusemets, V., Ivask, M., Teiter, S., Augustin, J., Mander, Ü. 2002. Budgets of nitrogen fluxes in riparian grey alder forests. Arch. Hydrobiol. 13(3–4), 321–332.

Lõhmus, K., Truu, M., Truu, J., Ostonen, I., Kaar, E., Vares, A., et al. 2006. Functional diversity of culturable bacterial communities in the rhizosphere in relation to fi ne-root and soil parameters in alder stands on forest, abandoned agricultural, and oil- shale areas. Plant Soil. 283(1–2), 1–10.

Lousier, J.D., Parkinson, D. 1976. Litter decomposition in a cool temperate deciduous forest. Can. J. Bot. 54, 419–436.

Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. Bioscience. 56, 395–405.

Lovett, G.M., Weathers, K.C., Arthur, M.A. 2002. Control of nitrogen loss from forested watersheds by soil carbon:nitrogen ratio and tree species composition. Ecosystems. 5(7), 712–718.

Lukac, M., Godbold, D.L. 2010. Fine root biomass and turnover in southern taiga estimated by root inclusion nets. Plant Soil. 331, 505–513.

Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, A., Hungate, B., McMurtrie, R.E., Oren, R., Parton, W.J., Pataki, D.E., Shaw, M.R., Zak, D.R., Field, C.B. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. Bioscience. 54, 731–739.

Luo, Y., Zhou, X. 2006. Soil respiration and the environment. Elsevier Academic Press, UK.

Magill, A.H., Aber, J.D., Berntso, G.M., McDowell, W.H., Nadelhoffer, K.J., Melillo, J.M., Staudler, P. 2000. Long-term nitrogen additions and nitrogen saturation in two temperate forests. Ecosystems. 3, 238–253.

Mäkinen H, Isomäki A, Hongisto T. 2006. Effect of half-systematic and systematic thinning on the increment of Scots pine and Norway spruce in Finland. Forestry. 79(1), 103–121.

Mäkinen H., Isomäki A. 2004b. Thinning intensity and long-term changes in increment and stem form of Norway spruce trees. Forest Ecol. Manag. 201(2), 295–309.

Mäkinen H., Isomäki A. 2004c. Thinning intensity and long-term changes in increment and stem form of Scots pine trees. Forest Ecol. Manag. 203(1), 21–34.

Mäkinen, H., Isomäki, A. 2004a. Thinning intensity and growth of Norway spruce stands in Finland. Forestry. 77(4), 349–364.

Mäkiranta, P., Laiho, R., Fritze, H., Hytönen, J., Laine, J., Minkkinen, K. 2009. Indirect regulation of heterotrophic peat soil respiration by water level via microbial community structure and temperature sensitivity. Soil Biol. Biochem. 41, 695–703.

Mäkiranta, P., Minkkinen, K., Hytönen, J., Laine, J. 2008. Factors causing temporal and spatial variation in heterotrophic and rhizospheric components of soil respiration in afforested organic soil croplands in Finland. Soil Biol. Biochem. 40, 1592–1600.

Maloney, D.C., Lamberti, G.A. 1995. Rapid decomposition of summer-input leaves in a northern Michigan stream. Am. Midl. Nat. 133, 184–195.

Mander, Ü., Maddison, M., Soosaar, K., Teemusk, A., Kanal, A., Uri, V., et al. 2015. The impact of a pulsing groundwater table on greenhouse gas emissions in riparian grey alder stands. Environ. Sci. Pollut. Res. 22(4), 2360–2371.

Martikainen, P.J., Nykänen, H., Grill, P., Silvola, J. 1993. Effect of a lowered water table on nitrous oxide fluxes from northern peatlands. Nature. 366, 51–53.

McClaugherty, C.A., Aber, J.D., Melillo, J.M. 1984. Decomposition dynamics of fine roots in forested ecosystems. Oikos. 42, 378–386.

McClaugherty, C.A., Pastor, J., Aber, J.D., Melillo, J.M. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology. 66, 266–275.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology. 59, 465–472.

Meentemeyer, V., Berg, B. 1986. Regional variation in rate of mass loss of Pinus sylvestris needle litter in Swedish pine forests as influenced by climate and litter quality. Scand. J. Forest. Res. 1, 167–180.

Melillo, J.M., Aber, J.D. 1984. Nutrient immobilization in decaying litter. In: Trends for ecological research in the 1980's. Edited by Cooley and Golley. NATO Conference Series, Ecology, Vol. 6. Plenum Press, New York. pp. 193–215.

Melillo, J.M., Aber, J.D., Muratore, J.M. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology. 63, 621–626.

Melillo, J.M., Aber, J.M., Linkins, A.E., Ricca, A., Fry, B., Nadelhoffer, K.J., 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. Plant Soil. 115, 189–198.

Meyer, A., Tarvainen, L., Nousratpour, A., Björk, R.G., Ernfors, M., Grelle, A., Kasimir Klemedtsson, Å., Lindroth, A., Räntfors, M., Rütting, T., Wallin, G., Weslien, P., Klemedtsson, L. 2013. A fertile peatland forest does not constitute a major greenhouse gas sink. Biogeoscience. 10, 7739–7758.

Miežite, O., Dreimanis, A. 2006. Investigations of grey alder (*Alnus incana* (L.) Moench) biomass. In: proceeding of the international scientific conference on research forest rural development, pp 271–275.

Millard, P., Sommerkorn, M., Grelet, G.-A. 2007. Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal. New Phytol. 175(1), 11–28.

Minkkinen, K., Korhonen, R., Savolainen, I., Laine, J. 2002. Carbon balance and radiative forcing of Finnish peatlands 1900–2100 – the impact of forestry drainage. Global Change Biology. 8(8), 785–799.

Minkkinen, K., Laine, J., Shurpali, N.J., Mäkiranta, P., Alm, J., Penttilä, T. 2007. Heterotrophic soil respiration in forestry-drained peatlands. Boreal Environ. Res. 12, 115–126.

Mund, M., Kummetz, E., Hein, M., Bauer, G.A., Schulze, E.D. 2002. Growth and carbon stocks of a spruce forest chronosequence in central Europe. Forest Ecol. Manag. 171, 275–296.

Nadelhoffer, K., Raich, J.W. 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology. 73, 1139–1147.

Nadelhoffer, K.J., Aber, J.D., Melillo, J.M. 1984. Seasonal patterns of ammonium and nitrate uptake in nine temperate forest ecosystems. Plant Soil. 80(3), 321–335.

Niemistö, P., Viherä-Aarnio, A., Velling, P., Heräjärvi, H., Verkasalo, E. (Eds.). 2008. Koivun kasvatus ja käyttö. Metla & Metsäkustannus, Karisto Oy, Hämeenlinna, Finland, pp. 1–254 (in Finnish).

Ojanen, P., Minkkinen, K., Alm, J., Penttilä, T. 2010. Soil-atmosphere CO2, CH4 and N2O fluxes in boreal forestry-drained peatlands. Forest Ecol. Manag. 260, 411–421.

Ostonen, I., Helmisaari, H.-S., Borken, W., Tedersoo, L., Kukumägi, M., Bahram, M. 2011. Fine root foraging strategies in Norway spruce forests across a European climate gradient. Glob. Change Biol. 17(12), 3620–3632.

Ostonen, I., Lõhmus, K., Pajuste, K. 2005. Fine root biomass, production and its proportion of NPP in a fertile middle-aged Norway spruce forest: comparison of soil core and ingrowth core methods. Forest Ecol. Manag. 212, 264–277.

Paal, J. 1998. Rare and threatened plant communities of Estonia. Biodivers. Conserv. 7, 1027–1049.

Pajuste, K., Frey, J. 2003. Nitrogen mineralisation in podzol soils under boreal Scots pine and Norway spruce stands. Plant Soil. 257(1), 237–247.

Palviainen, M., Finér, L., Kurka, A.M., Mannerkoski, H., Piirainen, S., Starr, M. 2004. Decomposition and nutrient release from logging

residues after clear- cutting of mixed boreal forest. Plant Soil. 263(1), 53–67.

Paul, K.I., Polglase, P.J., Richards, G.P. 2003. Predicted change in soil carbon following afforestation or reforestation, and analysis of controlling factors by linking a C accounting model (CAMFor) to models of forest growth (3PG), litter decomposition (GENDEC) and soil C turnover (RothC). Forest Ecol. Manag. 177, 485–501.

Persson, H. 1979. Fine-root production, mortality and decomposition in forest ecosystems. Vegetatio. 41, 101–109.

Persson, T., Bååth, E., Clarholm, M., Lundkvist, H., Söderström, B., Sohlenius, B. 1980. Trophic structure, biomass dynamics and carbon metabolism of soil organisms in a scots pine forest. Ecol. Bull. 32, 419–459.

Persson, T., Wirén, A. 1995. Nitrogen mineralization and potential nitrification at different depths in acid forest soils. Plant Soil. 168/169, 55–65.

Piirainen, S., Finér, L., Mannerkoski, H., Starr, M. 2007. Carbon, nitrogen and phorphorus leaching after site preparation at a boreal forest clear-cut area. Forest Ecol. Manag. 243(1), 10–18.

Pregitzer, K.S., Euskirchen, E.S. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Glob. Change Biol. 10, 2052–2077.

Prescott, C., Godbold, D.L., Helmisaari, H.-S., Addo-Danso, S.D. 2016. Introduction to Forests, roots and soil carbon. Forest Ecol. Manag. 359: 321.

Prescott, C.E. 2010. Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? Biogeochemistry. 101, 133–149.

Pussinen, A., Karjalainen, T., Mäkipää, R., Valsta, L., Kellomäki, S. 2002. Forest carbon sequestration and harvest in Scots pine stand under different climate and nitrogen deposition scenarios. Forest Ecol. Manag. 158, 103–115.

Püttsepp, Ü., Lõhmus, K., Koppel, A. 2007. Decomposition of fine roots and α- cellulose in a short rotation willow (*Salix* spp.) plantation on aban- doned agricultural land. Silva Fenn. 41(2), 247–258.

Raulo, J., Hokkanen, T. 1989. Harmaa-ja tervalepän karikesato. Summary: litter fall of *Alnus incana* and *Alnus glutinosa*. Folia For. 738, 25.

Repola, J., 2008. Biomass equations for birch in Finland. Silva Fenn. 42(4), 605–624.

Robertson, G.P., Vitousek, P.M. 1981. Nitrification potentials in primary and secondary succession. Ecology. 62, 376–386.

Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., et al. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia. 126, 543–562.

Rytter, L. 1996. The potential of grey alder plantation forestry. In: Perttu, K., Koppel, A. (eds). Short rotation willow coppice for renewable energy and improved environment. Swedish University of Agricultural Sciences, Uppsala, pp 89–94.

Rytter, L., Rytter, R.-M. 2016. Growth and carbon capture of grey alder (*Alnus incana* (L.) Moench.) under north European conditions – Estimates based on reported research. Forest Ecol. Manag. 373, 56–65.

Rytter, L., Šlapokas, T., Granhall, U. 1989. Woody biomass and litter production of fertilized grey alder plantations on a low-humified peat bog. Forest Ecol. Manag. 28, 161–176.

Rytter, R.M. 2013. The effect of limited availability of N or water on C allocation to fine roots and annual fine root turnover in *Alnus incana* and *Salix viminalis*. Tree Physiol. 33, 924–939.

Saarsalmi, A. 1995. Nutrition of deciduous tree species grown in short rotation stands. Dissertation, University of Joensuu, Finland.

Saiz, G., Byrne, K.A., Butterbach-Bahl, K., Kiese, R., Blujdea, V., Farrell, E.P. 2006. Stand age-related effects on soil respiration in a first rotation Sitka spruce chronosequence in Central Ireland. Glob. Change Biol. 12, 1007–1020.

Salm, J.O., Kimmel, K., Uri, V., Mander, Ü. 2009. Global warming potential of drained and undrained peatlands in Estonia: a synthesis. Wetlands. 29, 1081–1092.

Schimel, D.S., House, J.I., Hibbard, K.A., Bousquet, P., Ciais, P., Peylin, P., Braswell, B.H., Apps, M.J., Baker, D., Bondeau, A., Canadell, J.,

Churkina, G., Cramer, W., Denning, A.S., Field, C.B., Friedlingstein, P., Goodale, C., Heimann, M., Houghton, R.A., Melillo, J.M., Moore, B., Murdiyarso, D., Noble, I., Pacala, S.W. 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature. 414, 169–172.

Scott, A.N., Binkley, D. 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sites. Oecologia. 111, 151–159.

Silins, U., Rothwell, R.L. 1999. Spatial patterns of aerobic limit depth and oxygen diffusion rate at two peatlands drained for forestry in Alberta. Can. J. For. Res. 29(1), 53–61.

Silver, W.L., Miya, R.K. 2001. Global patterns in root decomposition: comparisons of climate the litter quality effects. Oecologia. 129, 407–419.

Silvola, J., Alm, J., Ahlholm, U., Nykänen, H., Martikainen, P.J., 1996. CO2 fluxes from peat in boreal mires under varying temperature and moisture conditions. J. Ecol. 84, 219–228.

Šlapokas, T. 1991. Influence of Litter Quality and Fertilization on Microbial Nitrogen Transformations in Short-Rotation Forests. Swedish University of Agricultural Sciences, Uppsala, Sweden (PhD dissertation).

Šlapokas, T., Granhall, U. 1991a. Decomposition of willow-leaf litter in a short-rotation forest in relation to fungal colonization and palatability for earthworms. Biol. Fert. Soils. 10, 241–248.

Šlapokas, T., Granhall, U. 1991b. Decomposition of litter in fertilized short-rotation forests on a low-humidified peat bog. Forest Ecol. Manag. 41(1-2), 143–165.

Soosaar, K., Mander, Ü., Maddison, M., Kanal, A., Kull, A., Lõhmus, K., Truu, J., Augustin, J. 2011. Dynamics of gaseous nitrogen and carbon fluxes in riparian alder forests. Ecol. Eng. 37(1), 40–53.

Staaf, H., Berg, B. 1982. Accumulation and release of plant nutrients in decomposing Scots pine needle litter. Long-term decomposition in a Scots pine forest. II. Can. J. Botany. 60, 1561–1568.

Sun, T., Dong, L., Zhang, L., Wu, Z., Wang, Q., Li, Y., Zhang, H., Wang, Z. 2016. Early stage fine-root decomposition and its relationship with root order and soil depth in a Larix Gmelinii plantation. Forests. 7(10): 234.

Sun, T., Mao, Z., Dong, L., Hou, Y., Wang, X. 2013. Further evidence for slow decomposition of very fine roots using two methods: litterbags and intact cores. Plant Soil. 366, 633–646.

Swift, M.J., Heal, O.W., Anderson, J.M. 1979. Decomposition in terrestrial ecosystems. Studies in ecology, Vol. 3. Berkeley/Los Angeles: Blackwell Scientific/University of California Press.

Tang, J., Bolstad, P.V., Martin, J.G. 2009. Soil carbon fluxes and stocks in a Great Lakes forest chronosequence. Glob. Change Biol. 15, 145–155.

Tate R.L. 1995. Soil microbiology. John Wiley & Sons, Inc, New York. 398 pp.

Telenius, B.F. 1999. Stand growth of deciduous pioneer tree species on fertile agricultural land in southern Sweden. Biomass Bioenergy. 16, 13–23.

Thibodeau, L., Raymond, P., Camiré, C., and Munson, A.D. 2000. Impact of precommercial thinning in balsam fir stands on soil nitrogen dynamics, microbial biomass, decomposition, and foliar nutrition. Can. J. For. Res. 30(2), 229–238.

Thorne, J.F., Hamburg, S.P. 1985. Nitrification potentials of an old-field chronosequence in Campton, New Hampshire. Ecology. 66, 1333–1338.

Tietema, A., Verstraten, J.M. 1992. Nitrate cycling in an acid forest ecosystem in the Netherlands under increased atmospheric nitrogen input. Biogeochemistry. 15, 21–46.

Uri, V., Aosaar, J., Varik, M., Becker, H., Ligi, K., Padari, A., Kanal, A., Lõhmus, K. 2014. The dynamics of biomass production, carbon and nitrogen accumulation in grey alder (*Alnus incana* (L.) Moench) chronosequence stands in Estonia. Forest Ecol. Manag. 327, 106–117.

Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., Aun, K., Krasnova, A., Morozov, G., Ostonen, I., Mander, Ü., Lõhmus, K., Rosenvald, K., Kriiska, K., Soosaar, K. 2019. The carbon balance of a six-year-old Scots pine (*Pinus sylvestris* L.) ecosystem estimated by different methods. Forest Ecol. Manag. 433, 248−262.

Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., Morozov, G., Karoles, K. 2017a. Ecosystems carbon budgets of differently aged

downy birch stands growing on well-drained peatlands. Forest Ecol. Manag. 399, 82–93.

Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., Soosaar, K., Morozov, G., Ligi, K., Padari, A., Ostonen, I., Karoles, K. 2017b. Carbon budgets in fertile grey alder (*Alnus incana* (L.) Moench.) stands of different ages. Forest Ecol. Manag. 396, 55–67.

Uri, V., Lõhmus, K., Kiviste, A., Aosaar, J. 2009. The dynamics of biomass production in relation to foliar and root traits in a grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural land. Forestry. 82, 61–74.

Uri, V., Lõhmus, K., Kund, M., Tullus, H. 2008. The effect of land use on net nitrogen mineralization on abandoned agricultural land: silver birch stand versus grassland. Forest Ecol. Manag. 255(1), 226–233.

Uri, V., Lõhmus, K., Mander, Ü., Ostonen, I., Aosaar, J., Maddisson, M., Helmisaari, H.-S., Augustin, J. 2011. Long-term effects on nitrogen budget of a short-rotation grey alder (*Alnus incana* (L.) Moench) forest in abandoned agricultural land. Ecol. Eng. 37, 920–930.

Uri, V., Lõhmus, K., Ostonen, I., Tullus, H., Lastik, R., Vildo, M. 2007. Biomass production, foliar and root characteristics and nutrient accumulation in young silver birch (*Betula pendula* Roth.) stand growing on abandoned agricultural land. Eur. J. For. Res. 126(4), 495–506.

Uri, V., Lõhmus, K., Tullus, H. 2003. Nutrient allocation, accumulation and aboveground biomass in grey alder and hybrid alder plantations. Silva Fenn. 37(3), 301–311.

Uri, V., Tullus, H., Lõhmus, K. 2002. Biomass production and nutrient accumulation in short-rotation grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural land. Forest Ecol. Manag. 161(1–3), 169–179.

Uri, V., Varik, M., Aosaar, J., Kanal, A., Kukumägi, M., Lõhmus, K. 2012. Biomass production and carbon sequestration in a fertile silver birch forest chronosequence. Forest Ecol. Manag. 267, 112–126.

Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, U., Berbigier, P., Loustau, D., Gümundsson, J., Thorgeirsson, H., Ibrom, A.,

Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G. 2000. Respiration as the main determinant of carbon balance in European forests. Nature. 404(6780), 861–865.

Van Praag, H.J., Weissen, F. 1973. Elements of a functional definition of oligotrophic humus based on the nitrogen nutrition of forest stands. J. Appl. Ecol. 10(2), 569–583.

Vanninen, P., Mäkelä, A. 1999. Fine root biomass of Scots pine stands differing in age and soil fertility in southern Finland. Tree Physiol. 19, 823–830.

Vares, A. 2001. Sanglepa (*Alnus glutinosa* (L.) Gaertn.) lehevarise lagunemine ja lämmastiku dünaamika Eesti kliimatingimustes [Decomposition and nitrogen dynamics in black alder (*Alnus glutinosa* (L.) Gaertn.) leaf litter in the climatic conditions in Estonia]. Metsanduslikud uurimused. 35, 149–155. Estonian.

Varik, M., Aosaar, J., Ostonen, I., Lõhmus, K., Uri, V. 2013. Carbon and nitrogen accumulation in belowground tree biomass in a chronosequence of silver birch stands. Forest Ecol. Manag. 302, 62–70.

Varik, M., Kukumägi, M., Aosaar, J., Becker, H., Ostonen, I., Lõhmus, K., Uri, V. 2015. Carbon budgets in fertile silver birch (*Betula pendula* Roth) chronosequence stands. Ecol Eng. 77, 284–296.

Verlinden, M.S., Broeckx, L.S., Zona, D., Berhongaray, G., De Groote, T., Camino Serrano, M., et al. 2013. Net ecosystem production and carbon balance of an SRC poplar plantation during its first rotation. Biomass Bioenerg. 56, 412–422.

von Arnold, K., Nilsson, M., Hånell, B., Weslien, P., Klemedtsson, L. 2005a Fluxes of CO2, 1067 CH4 and N2O from drained organic soils in deciduous forests, Soil Biol. Biochem. 37(6), 1059–1071.

von Arnold, K., Weslien, P., Nilsson, M., Svensson, B.H., Klemedtsson, L. 2005b. Fluxes of 1070 CO2, CH4 and N2O from drained coniferous forests on organic soils. Forest Ecol. Manag. 210, 239–254.

Walle, I.V., Van Camp, N., Van de Casteele, L., Verheyen, K., Lemeur, R. 2007. Short rotation forestry of birch maple, poplar and willow in Flanders (Belgium). I – biomass production after 4 years of tree growth. Biomass Bioenerg. 31, 267–275.

Wang, C.K., Bond-Lamberty, B., Gower, S.T. 2002. Soil surface CO2 flux in a boreal black spruce fire chronosequence. J. Geophys. Res. 107, 8224.

Waring, R.H., Running, S.W. 2007. Forest Ecosystems: Analysis at Multiple Scales, third ed. Academic Press, San Diego, pp. 263–291.

Westman, C.J., Laiho, R. 2003. Nutrient dynamics of drained peatland forests. Biogeochemistry. 63(3), 269–298.

Wiseman, P.E., Seiler, J.R. 2004. Soil CO2 efflux across four age classes of plantation loblolly pine (*Pinus taeda* L.) on the Virginia Piedmont. Forest Ecol. Manag. 192, 297–311.

Wu, J., Larsen, K.S., van der Linden, L., Beier, C., Pilegaard, K., Ibrom, A. 2013. Synthesis on the carbon budget and cycling in a Danish, temperate deciduous forest. Agric. Forest Meteorol. 181, 94–107.

Wu, Z., Dijkstra, P., Koch, G.W., Peñuelas, J., Hungate, B.A. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta- analysis of experimental manipulation. Glob. Change Biol. 17, 927–942.

Xiong, Y., Fan, P., Fu, S., Zeng, H., Guo, D. 2013. Slow decomposition and limited nitrogen release by lower order roots in eight Chinese temperate and subtropical trees. Plant Soil. 363, 19–31.

Yearbook Forest. 2016. Compiled by Estonian Environmental Information Centre. Tartu 2017. In Estonian. [accessed 2017 Nov 4]. http://www.keskkonnaagentuur.ee/sites/default/files/mets2016_08. 08.pdf.

Zak, D.R., Grigal, D.R., Gleeson, S., Tilman, D. 1990. Carbon and nitrogen cycling during old-field succession: constraints on plant and microbial biomass. Biochemistry. 11(2), 111–129.

Zhang, Q., Wang, C., Wang, X., Quan, X. 2009. Carbon concentration variability of 10 Chinese temperate tree species. Forest Ecol. Manag. 258(5), 722–727.

SUMMARY IN ESTONIAN

SÜSINIKU- JA LÄMMASTIKUVOOD ERINEVATE KASVUKOHTADE KAASIKUTES JA HALL-LEPIKUTES

Suurenenud atmosfäärse CO_2 kontsentratsiooni ja sellest tulenevate kliimamuutuste taustal on boreaalse ja hemiboreaalse vööndi metsadel täita oluline roll süsiniku (C) sidujatena ja seeläbi kliimamuutuste leevendajatena (Dixon et al. 1994, Valentini et al. 2000, Liski et al. 2002, 2003, Gough et al. 2008). Ka Eesti on ühinenud Pariisi kliimaleppega (2015) ja peab lähitulevikus koos teiste riikidega vähendama C emissiooni. Siinkohal on metsad olulised nii C sidujatena kui ka taastuva energiaallikana. Metsad seovad C nii puude biomassis kui ka mullas (Cannell 1999, Mund et al. 2002, Pussinen et al. 2002, Ågren and Hyvonen 2003, Laiho et al. 2003). Et metsade C varu muutumine võib mõjutada C sisaldust atmosfääris (Keith et al. 2009), on C bilansi hindamine erinevates ökosüsteemides oluline ka globaalsel tasandil.

Metsad on aga äärmiselt heterogeensed, nende C sidumine sõltub suurel määral puuliigilist, kasvukohast, puistu vanusest ja veel paljudest teguritest. Metsateaduses on aktuaalseks valdkonnaks C sidumise kvantitatiivne hindamine erinevates puistutes, samuti C sidumist mõjutavate faktorite selgitamine (Fang *et al.* 2007). Nende hulgas on mulla lämmastiku (N) sisaldus üks neist tegureist, mis suurel määral mõjutab metsa produktsioonivõimet ja seeläbi ka C sidumist ökosüsteemi tasandil: suureneva CO_2 kontsentratsiooni juures hakkab puude edasist produktsiooni tõusu piirama eelkõige N kättesaadavus (Feng *et al.* 2015); seega on C ja N ringed metsaökosüsteemides omavahel tihedalt seotud.

Oluline protsess orgaanilise varise ning mulla CN varude vahel on orgaanilise aine lagunemine. Töös uuriti halli lepa ja arukase lehe- ja juurevarise lagunemise pikaajalist dünaamikat, mis võimaldab hinnata lagunemise käigus mulda jõudvat CN kogust ja lagunemise kiirust (**I**). Kuna taimse materjali lagunemisel vabanevad selles seotud toitained (sh. N), siis on sellel protsessil oluline mõju biomassi produktsioonile ja seeläbi C sidumisele.

Hall-lepikud on kiirekasvulised ja perspektiivsed energiametsadena (Uri et al. 2011; 2014; Rytter & Rytter 2016). Põhja- ja Baltimaades läbiviidud

uuringud on näidanud hall-lepikute kõrget produktsioonivõimet nii mineraal- kui turbamuldadel (Granhall & Verwijst 1994; Saarsalmi 1995; Rytter 1996; Telenius 1999; Miezite 2008; Hytonen & Saarsalmi 2010), kuid samas on need puistud C bilansi seisukohalt praktiliselt uurimata. Aga kaasaja metsandus peab olema teaduspõhine ning ei saa soovitada selliste puistute ulatuslikku kasvatamist, mille puhul pole hinnatud võimalikke kaasnevaid keskkonnamõjusid. Juhul kui CO_2 bilanss hall-lepikutes oleks negatiivne, ei saaks rääkida neist kui „rohelise energia" ressursist. Et selgitada C bilansi dünaamikat erivanuselistes hall-lepikutes ja seega nende rolli regionaalses C bilansis laiemalt, hinnati töös peamised C sisend- ja väljundvood erineva vanusega hall-lepikutes (**III**).

Kuivendatud soodes kasvavate metsade puhul on üheks olulisemaks küsimuseks C bilanss nendes ökosüsteemides. Ühelt poolt suureneb peale kuivendamist C emissioon turvasmuldadest, kuid teisalt paraneb ka nendel aladel kasvavate metsade juurdekasv, st. C sidumine. Võtmeküsimuseks on nende kahe C voo omavaheline tasakaal, st. kas puude suurenenud juurdekasv katab ja ületab mulla orgaanilise aine lagunemise käigus tekkiva C voo või mitte, st. kas metsaökosüsteem on C allikas või C siduja. Töös koostati C bilansid viie erineva vanusega sookaasiku kohta ja nende põhjal hinnati taoliste puistute toimimist kliima soojendajate või jahutajatena (**IV**).

Paranenud aeratsiooni- ning lagunemistingimused kuivendatud turvasmuldades avaldavad mõju ka lämmastiku netomineralistasiooni (NNM) protsessile. Töös hinnati aastase NNM voo dünaamikat ja intensiivsust ning selgitati suurenenud omastatava N sisalduse mõju puude produktsioonivõimele ja C sidumisele (**II**).

Boreaalsetes ja parasvöötme metsades on NNM üks peamisi lämmastiku transformatsiooniprotsesse mullas, mille käigus muudetakse orgaaniline N taimedele omastatavaks mineraalseks lämmastikuks (Luo *et al*. 2004), kuid erinevate metsamajanduslike tegevuste mõju metsade N ringele on suhteliselt vähe uuritud valdkond. Käesolevas töös hinnati harvendusraiete mõju arukaasikus mulla NNM ja N leostumise voogudele (**V**).

Töö põhieesmärgid:

1. hinnata lehe- ja juurevarise pikaajalist lagunemise dünaamikat noortes halli lepa ja arukase puistutes. Samuti hinnata varisekottide meetodi sobivust lagunemiskatseteks viljakates kasvukohtades (**I**);

2. analüüsida C bilansi meetodil süsinikuringe dünaamikat erivanustes kõdusoomuldadel kasvavates sookaasikutes. Samuti hinnata nendes metsades aastast N netomineralisatsiooni (NNM) voogu ning selgitada selle mõju puistu C sidumisele (**IV** ja **II**);

3. hinnata viljakatel muldadel kasvavate erivanuseliste hall-lepikute C sidumise dünaamikat ökosüsteemi tasandil, kasutades C bilansi meetodit (**III**), mis võimaldab selgitada nende puistute rolli regionaalses C bilansis;

4. hinnata harvendusraie mõju aastasele NNM intensiivsusele ning N leostumisele noores arukaasikus (**V**).

Töös püstitati järgmised hüpoteesid:

1. Tingituna kõrgemast N sisaldusest ning madalamast C:N suhtest lagunevad nii lepa lehe- kui ka juurevaris sarnastel muldadel kasvavates puistutes kiiremini kui kase vastavad varisefraktsioonid (**I**);

2. Kuivendatud turvasmuldadel kasvavad sookaasikud on C-d siduvad ökosüsteemid, kuna paranenud kasvutingimused, sh. suur omastatava N sisaldus mullas (**II),** suurendavad puude biomassi produktsiooni ja tänu sellele C sidumine ületab heterotroofsest mullahingamisest tuleneva süsinikukao (**IV**);

3. Hall-lepikud on efektiivsed C-d siduvad metsaökosüsteemid, kusjuures süsiniku sidumine on suurem nooremates metsades ning kahaneb puistu vananedes (**III**);

4. Pärast harvendusraiet intensiivistub aastane N netomineralisatsioon, mis on tingitud mullatemperatuuri tõusust; samuti suureneb N leostumine, mis omakorda on tingitud nitraatlämmastiku sisalduse suurenemisest mullas (**V**).

Metoodika

Katsealad

Käesolev töö põhineb erinevates halli lepa ja kase puistutes tehtud uuringutel.

Lehe- ja juurelagunemise katse viidi läbi endise põllumaa hall-lepikus ja arukaasikus (Tabel 1, **I**). Süsinikubilansi uuringuteks valiti välja viis loodusliku tekkega hall-lepikut vanuses 7 kuni 38 aastat, kuhu rajati püsikatsealad (Tabel 1, **III**). Need puistud olid erineva maakasutuse ajalooga, kaks neist kasvasid endistel põllumaadel ja kolm metsamaal.

Kuivendatud metsade C bilansi dünaamika selgitamiseks rajati katsealad viide erineva vanusega (12-78 aastat) kõdusoo kaasikusse (Tabel 1, **IV**). Neist keskealises (30-aastane) sookaasikus viidi läbi ka N netomineralisatsiooni (NNM) katse (Tabel 1, **II**).

Harvendusraie mõju NNM-le (Tabel 1, **V**) hinnati endisel põllumaal kasvavas arukaasikus, samas puistus viidi läbi ka lehtede ja juurte lagunemiskatse (**I**).

*Lehtede ja juurte lagunemine (**I**)*

Lagundamiskatseks korjati lehevaris samast puistust ja kuivatati +70 °C juures püsiva kaaluni. Ka juured kaevati välja samadest puistutest, kuhu lagunemiskatse inkubeeriti. Juured pesti enne kuivatamist hoolikalt, puude (kask, lepp) juurtest eraldati rohttaimede juured ja puude surnud juured. Leheproovid pakiti võrgust varisekottidesse (15x15 cm), võrgu silma läbimõõt oli 1mm. Juureproovid pakiti 5x5 cm kottidesse, silma läbimõõduga 0,14 mm. Iga kott varustati plastiksedeliga, millel oli kirjas proovi number. Nii lehe- kui juureproovid ühendati omavahel kümnekaupa nööriga ja inkubeeriti katsealale (lehed maapinnale, juured mulla ülemisse 5–10 cm kihti).

Lehtede lagunemiskatse kestis 4 aastat, selle aja jooksul võeti proove kümnel korral, iga kord keskmiselt 9 proovi. Laboris proovid avati, puhastati mullast ja sissekasvanud juurtest, seejärel kuivatati ning

kaaluti. Proovidest analüüsiti tuhasisaldus ning lämmastiku ja fosfori kontsentratsioon. Juureproovide kogumine ja töötlemine toimus sarnaselt, kuid katse kestvus oli oluliselt pikem, lepajuurtel 11 aastat ning kasejuurtel 9 aastat.

*Lämmastiku netomineralisatsiooni katsed (**II, V**)*

Lämmastiku netomineralisatsiooni voo hindamiseks kasutati maetud kilekottide meetodit (Eno 1960), mida töörühm on kasutanud ka mitmetes varasemates töödes (Uri et al. 2003, 2008, 2011; Becker et al. 2015, 2016); meetodi detailsem kirjeldus on toodud artiklites (**II, V**). Meetod põhineb regulaarsel mullaproovide inkubeerimisel ja erinevate N vormide sisalduse määramisel. Mullaproove võeti igakuiselt ning neist analüüsiti mineraalse N sisaldus, samuti inkubeeriti igal korral uued proovid. Kilekotti pakitud mullaproovis toimub mineralisatsiooniprotsess looduslikele lähedastes tingimustes, samas on välditud N omastamine taimede poolt ning leostumine.

*Süsiniku ja lämmastiku leostumine (**III, V**)*

Et hinnata CN leostumist, kasutati roostevabast terasest plaatlüsimeetreid (kogumispindalaga 627 cm^2), mis paigutati juhuslikult katsealadele, 40 cm sügavusele. Lüsimeetrist voolas leostunud vesi ca 1 meetri sügavusele paigutatud 6000 ml kanistrisse. Hall-lepikutes oli katsealal 10 lüsimeetrit, arukaasikus mõlemas katsevariandis (harvendatud *versus* kontroll) 7 lüsimeetrit. Leostunud vett koguti spetsiaalse vaakumpumbaga üks kord kuus, kevadest kuni maapinna külmumiseni. Kogutud vee hulk mõõdeti ning proovidest analüüsiti erinevate CN vormide sisaldus.

*Süsinikubilanss (**III, IV**)*

Süsinikubilansi koostamiseks hinnati erinevates puistutes peamised C sisend- ja väljundvood (**III**, **IV**). Ökosüsteemis seotud süsinik (NEP) leiti primaarproduktsiooni (NPP) ning heterotroofse mullahingamise (Rh) ja leostumise (L) vahena (Clark et al. 2001, Lovett et al. 2006, Meyer et al. 2013):

$$NEP = NPP - (Rh + L)$$

NPP arvutamiseks liideti taimede (puud ja alustaimestik) aastases produktsioonis seotud C.

NEP positiivse väärtuse korral on tegemist C siduva ökosüsteemiga, negatiivse korral aga C allikaga st. NEP iseloomustab ökosüsteemis seotud või kaotatud C kogust (Chapin *et al.* 2006, Waring & Running 2007).

Mulla ja taimse materjali keemilised analüüsid

Mullaprofiili kirjeldamiseks ja mullaliigi määramiseks kaevati igale alale vähemalt üks 1 m sügavune mullakaeve. Mullaliigi määramisel kasutati WRB klassifikatsiooni (WRB 2006). Aladel, kuhu paigaldati lüsimeetrid (lepikud, kaasik), tehti vastavalt 10 ja 14 kaevet. Kaevetest võetud proovide põhjal määrati mulla mahukaal erinevate sügavuskihtide kaupa.

Mulla C ja toitainete varude hindamiseks võeti mullapuuriga igalt katsealalt 10-15 juhuslikust punktist proovid, mulla erinevatest sügavuskihtidest 10 cm kaupa kuni 50 cm sügavuseni. Kihtide kaupa koondati proovid koondproovideks (vähemalt 3 proovi kihi kohta), kust määrati toitainete sisaldus, mulla pH ning C sisaldus.

Statistilised meetodid

Valimite normaaljaotust kontrolliti Lilleforsi ja Shapiro-Wilki testidega. Erinevate faktorite mõju hindamiseks rakendati dispersioonanalüüsi (ANOVA). Dispersioonanalüüsi puhul kontrolliti valimite homogeensust Levene testiga. t-testi rakendati kahe valimi keskmiste võrdluseks. Mediaanide võrdlemisel rakendati Wilcoxon Matched Pairs testi. Keskmise C ning toitainete kontsentratsiooni võrdlemisel kasutati Tukey HSD testi. Tunnuste omavaheliste seoste leidmiseks kasutati korrelatsioonanalüüsi. Lineaarseid ja allomeetrilisi mudeleid rakendati tunnuste vaheliste seoste leidmiseks. Mudeli sobivust hinnati korrigeeritud determinatsioonikordaja (R^2) ja olulisuse tõenäosuse (P) alusel. Kõigil juhtudel kasutati olulisuse tõenäosuseks 0.05. Statistiliste arvutuste tegemisel kasutati programmi STATISTICA 7.0.

Tulemused ja arutelu

Lehtede ja juurte lagunemine

Erinevate juurefraktsioonide lagunemise dünaamika oli uuritud puuliikide puhul sarnane: mõlemal juhul oli peenemate (d<2mm) juurte lagunemine oluliselt aeglasem jämedamate (2<d<5 mm) juurte lagunemisest (**I**). See tulemus on osaliselt seletatav kõrgema ligniinisisaldusega peenemates juurtes. Jämedamates juurtes oli suurem tselluloosisisaldus, mis on erinevate mikroorganismide poolt kiiremini lagundatav.

Leheproovide lagunemiskiirus oli ligi kolm korda intensiivsem kui juureproovidel, mistõttu vabanes lehevarisest C ja N ka kiiremini aineringesse. Koguseliselt jõudis uuritud arukase ning halli lepa puistutes lehevarisest mulda lämmastikku 7-14 korda rohkem kui juurevarisest.

Seega ei leidnud püstitatud hüpotees kinnitust: kõrgema N sisaldusega halli lepa lehed ja juured ei lagunenud kiiremini arukase vastavatest fraktsioonidest.

Kasutatud varisekottide meetod ei kajastanud tegelikku orgaanilise aine lagunemise kiirust viljakates kasvukohtades. Halli lepa ja arukase leheproovidest oli pärast kolm aastat lagunemist varisekottides säilinud ligikaudu 20% nende algsest massist. Kui lehe ja juurevaris tõesti nii aeglaselt laguneksid, siis peaks neis puistutes olema kujunenud tüse kõduhorisont. Varisekottides on orgaanilise aine lagunemine takistatud, kuna neisse ei pääse mulla makro- ja mesofauna esindajad. Samuti mõjutab varisekottide võrk substraadi kontakti mullaga, mille tulemusena ei püsi niiskus ega temperatuur lagunevas materjalis stabiilsena, mis muudab keskkonna lagundajate jaoks ebasobivamaks.

Varisekottide meetod on tõenäoliselt sobivam kasutamiseks kasvukohtades, kus lagundajateks on eelkõige mikroorganismid ja seened ning mullafauna (vihmaussid) osakaal on väike (näiteks väheviljakad kasvukohad). Samuti annaks see meetod võrreldavaid tulemusi erinevate substraatide lagunemiskiiruse võrdlemiseks sarnastes tingimustes.

Kuivendatud sookaasikute süsinikubilanss

Jänesekapsa-kõdusoo mullad on reeglina kõrge viljakusega ning samas ka suure C varuga. Kuivendatud turvasmuldadel kasvavad noored sookaasikud osutusid efektiivseteks C-d siduvateks puistuteks (**IV**). See oli tingitud puistute kõrgest biomassi produktsioonist, mis ületas oluliselt heterotroofsest mullahingamisest (Rh) tuleva C emissioonivoo. Aastane Rh voog varieerus uuritud puistutes vahemikus 4,7 kuni 6,2 t C ha^{-1} ja ei sõltunud puistu vanusest ega turbahorisondi tüsedusest. Kuigi kuivendatud turvasmuldade puhul eeldatakse intensiivistunud Rh voogu, jäi see käesolevas töös samasse suurusjärku (2-6 t C ha^{-1} a^{-1}) mineraalmuldadel kasvavatest puistutest mõõdetuga (Kukumägi *et al.* 2017; Uri *et al.* 2017a, Varik *et al.* 2015).

Kuna mullahingamisest eralduv C voog oli erineva vanusega puistutes samas suurusjärgus ja seotud C akumuleerus peamiselt puude biomassis, siis on selliste metsade majandamisel maksimaalse C sidumise seisukohalt oluline optimaalse raieringi rakendamine, samuti sookasest produktiivsemate puuliikide (kuusk, sanglepa) kasvatamine.

Ilmnes vanuse mõju puistute süsinikubilansile: kui noored puistud olid olulised C sidujad, siis keskealise sookaasiku (38 a.) süsinikubilanss oli tasakaalus. Kõige vanemas sookaasikus (78 a.) ületas aastane Rh voog C sidumise ja see puistu oli C allikas.

Mulla C bilanss oli kõikides puistutes negatiivne, st. aastane orgaanilise C sisendvoog mulda (maapealne, maa-alune ja alustaimestik) oli väiksem kui aastane Rh voog, mis näitab pidevat turba lagunemist ning süsinikuvaru vähenemist mullas.

Aastane lämmastiku netomineralisatsiooni voog kuivendatud sookaasikus

Ökosüsteemi C ja N ringed on omavahel tihedalt seotud: biomassi produktsiooni oluline mõjutaja on mineraalse N sisaldus mullas (**II**). Aastast N netomineralisatsiooni (NNM) voogu mõjutab ühelt poolt mulla orgaanilise N sisaldus, samuti ka CN suhe ning mulla happesus. Teisalt sõltub NNM intensiivsus maapealse varise koostisest ja kogusest. Kõrge aastane NNM voog (127,5 kg N ha^{-1} a^{-1}) viitab sellele, et pikka aega kuivendatud madalsoomullad on sarnaselt mineraalmuldadele

kõrge omastatava N sisaldusega, tagades puistu kõrge produktsiooni ja C sidumise.

Erivanuseliste hall-lepikute süsinikubilanss

Hall-lepikud on kiirekasvulised ja suure produktsioonivõimega puistud, mis omavad potentsiaali energiapuistutena (Granhall & Verwijst 1994; Saarsalmi 1995; Rytter 1996; Telenius 1999; Miežite 2008; Hytönen & Saarsalmi 2009). Noored ja keskealised hall-lepikud osutusid efektiivselt süsinikku siduvateks ökosüsteemideks, akumuleerides 1-4 t C ha^{-1} a^{-1} (**III**). Vanim uuritud puistutest (40 a.), osutus aga nõrgaks C allikaks, emiteerides 0,8 t C ha^{-1} a^{-1}. Mitme aasta jooksul läbi viidud uurimuses avaldus aasta e. ilmastiku mõju puistute produktsioonile ja C sidumisele (Tabelid 4 ja 9, **III**). Raiesmikel uuenenud noor hall- lepik võib ebasoodsal aastal olla isegi C allikas (-2 t ha^{-1} a^{-1}), kuid soodsal aastal C siduja (+1 t C ha^{-1} a^{-1}). Sellistes kasvukohtades on suur mõju eelmisest metsapõlvkonnast pärit laguneva orgaanilise aine kogusel (kännud, juured, raiejäätmed), mis suurendab C emissiooni mullast. Saadud tulemused näitavad ka pikemaajaliste C uuringute olulisust, sest vaid ühel aastal läbi viidud hindamised võivad olla tugevalt mõjutatud konkreetse aasta ilmastikust.

Koostatud C bilansid näitasid C sidumist valdavalt puude biomassis, kuid endisele põllumaale tekkinud hall-lepikus seoti C ka mulda. See tulemus on heas kooskõlas varasema tööga kus samuti leiti, et põlistel metsamaadel mulla C sisaldus puistu eluea jooksul ei suurenenud (Uri *et al.* 2014).

Kuna C seotakse puude biomassis ja kuna varisega (maapealne, maa-alune) mulda jõudva orgaanilise C kogus on samas suurusjärgus aastase Rh vooga, siis seda tuleb arvestada nende puistute majandamisel, st. mahuküpsusest lähtuv soovituslik raievanus (20-25 a.) tagab ühtlasi C efektiivse majandamise.

Harvendusraie mõju lämmastiku mineralisatsiooni ja leostumise voole

Harvendusraie arukaasikus suurendas aastast NNM voogu, mõjutades eelkõige nitrifikatsiooni intensiivsust (**V**). Harvendamise positiivne mõju N mineralisatsioonile osutus lühiajaliseks ning juba teisel raiejärgsel aastal NNM vood kontrollalal ja harvendatud alal enam ei erinenud. Kuna

antud arukase puistu on pikaajalise uurimisajalooga ning viimase 13 aasta jooksul on selles läbi viidud kolm NNM katset erinevatel perioodidel, siis ilmnes aastase NNM voo vähenemine puistu vanuse suurenedes. Kui noores (8 a.) puistus oli aastane NNM voog mulla ülemises 10 cm kihis 99 kg N ha^{-1} a^{-1}, siis kümme aastat hiljem oli see 52 kg N ha^{-1} a^{-1} ning 21-aastases puistus vaid 30 kg N ha^{-1} a^{-1}. See trend on tõenäoliselt seletatav maakasutuse ajalooga ja endise põllumaal metsa arenemisega kaasneva tendentsiga.

Aastane N leostumine oli arukaasikus väike ning harvendusraie seda ei suurendanud. Kontrollalal oli leostunud N kogus isegi suurem, mis tulenes peamiselt suuremast nõrgvee kogusest. Tõenäoliselt mõjutas sademetevee jõudmist alumistesse mullakihtidesse alustaimestiku suurem katvus harvendatud alal.

Kokkuvõte

Doktoritöös hinnati süsiniku (C) ja lämmastiku (N) erinevaid voogusid ning varusid hall-lepikutes ja kaasikutes. Uuritud puistud kasvasid viljakatel mineraal- ja turvasmuldadel ning olid produktiivsed.

1. Kuigi halli lepa lehe- ning juurevarises oli N sisaldus kõrgem kui arukase vastavas fraktsioonis, polnud nende lagunemiskiirus oluliselt erinev. Samuti ei erinenud halli-lepa ja arukase vastavate juurefraktsioonide lagunemiskiirus. Küll aga lagunesid mõlema uuritud puuliigi puhul peenemad juured ($d<2mm$) aeglasemalt kui jämedamad ($2<d<5mm$). Seega ei leidnud töös püstitatud hüpotees kinnitust: varise lagunemise kiirus ei sõltunud puuliigist.

Väike osa juurevarisest oli varisekottides äratuntaval kujul alles veel ka pärast 10 a. pikkust lagunemisperioodi. See näitab, et kasutatud meetod ei peegelda tegelikku, looduslikus keskkonnas kulgevat protsessi. Aeglasem lagunemine on tingitud peamiselt sellest, et oluline osa mullafaunast ei pääse lagundatava orgaanilise materjalini. Meetod oleks rakendatav erinevate proovide lagunemise dünaamika võrdlevaks hindamiseks sarnastes tingimustes. Tõenäoliselt sobiks meetod paremini lagunemiskatsete läbiviimiseks kasvukohtades, kus mullafaunat (ennekõike vihmausse) esineb vähem (madalama viljakusega kasvukohad).

2. Kinnitust leidis teine hüpotees: noored ja keskealised sookaasikud jänesekapsa kõdusoos olid kas C-d siduvad ökosüsteemid või oli C bilanss neis tasakaalus. Noortes puistutes ületas aastane biomassis seotud C mulla heterotroofse hingamise (Rh) voogu, st. C bilanss oli positiivne. Keskealises (38-aastane) sookaasikus oli aastane C sidumine samas suurusjärgus mullahingamisega, mis näitab tasakaalus C bilanssi, st. selline puistu on C neutraalne. Vaid vanim, 78-aastane kaasik oli C-d kaotav ökosüsteem.

Aastane (Rh) voog oli erineva vanusega ja erineva turba tüsedusega aladel samas suurusjärgus. Veelgi enam, käesolevas töös mõõdetud aastased Rh vood jäävad samasse suurusjärku erinevatel mineraalmuldadel kasvavates metsades mõõdetuga. Kuid kõikides uuritud sookaasikutes ületas aastane Rh voog varise (lehed, juured, alustaimestik) kaudu mulda jõudnud orgaanilise C voo, mis näitab negatiivset mulla C bilanssi, st. muld kaotab jätkuvalt C varu.

Metsade C ja N ringed on omavahel tihedalt seotud. Aastane NNM voog jänesekapsa kõdusoo kaasikus oli kõrge (127,5 kg N ha^{-1} a^{-1}), tagades mineraalse N hea kättesaadavuse taimede jaoks ning seeläbi puistude kõrge produktsiooni ning C sidumise.

3. Erivanuseliste hall-lepikute C bilansi dünaamika toetas osaliselt püstitatud hüpoteesi: vanim uuritud hall-lepik osutus C allikaks, samas kui noored ja keskealised puistud olid üldjuhul C-d siduvad. Erandina oli ühel aastal ka noorimas (7 a.) puistus C bilanss negatiivne, mis on ühelt poolt põhjendatav maakasutuse ajalooga: see lepik kasvas endisel lageraieraiesmikul, kus esinev suur kogus lagunevat orgaanilist materjali (kännud, juured, raiejäätmed) suurendas C emissioonivoogu. Teisalt mängis olulist rolli ebasoodne ilmastik ja sellest tingitud puude tagasihoidlik produktsioon. Erinevate aastate ilmastik võib C bilanssi oluliselt mõjutada: järgmisel aastal oli sama lepik C-d siduv ökosüsteem. Seega tagavad mitmeaastased kordusmõõtmised samas puistus usaldusväärsemaid C voogude hinnanguid, sest aastate lõikes võib puistu produktsioon ja aastane C sidumine oluliselt varieeruda.

Saadud tulemused on kooskõlas varasemate töödega, mis näitavad maakasutuse mõju C sidumisele puistutes. Esimese põlvkonna lepikutes, mis kasvavad mittemetsamaadel (endised põllumaad, ammendatud liiva-

ja kruusakarjäärid), seoti C nii puude biomassi kui ka mulda. Metsamaadel kasvavates lepikutus salvestus C peamiselt vaid puude biomassis.

4. Harvendusraie suurendas NNM intensiivsusest arukaasikutes, kuid see mõju oli lühiajaline. Harvendamine suurendas peamiselt nitrifikatsiooni intensiivsust, ammonifikatsiooni voog ei erinenud kontrollalal ja harvendatud alal. N leostumine harvendatud puistus oli väiksem kui kontrollalal, mis tulenes peamiselt suuremast nõrgvee kogusest. Tõenäoliselt mõjutas sademetevee jõudmist alumistesse mullakihtidesse alustaimestiku suurem katvus harvendatud alal.

Metsanduslikud hinnangud ja soovitused

Töös kasutatud publikatsioonidest kaks (I ja II) käsitlevad mullas toimuvaid transformatsiooniprotsesse (orgaanilise aine lagunemine ja lämmastiku netomineralisatsioon) ning need tööd kuuluvad pigem alusuuringute valdkonda.

Kolme uurimistöö (III IV V) tulemuste põhjal saab anda mõningaid metsanduslikke hinnanguid või soovitusi praktikas rakendamiseks.

Kuna lähitulevikus võib prognoosida hall-lepikute intensiivsemat kasutust ja nende metsamajandusliku tähtsuse suurenemist rohelise energia allikana, siis on vaja hinnata nende puistute majandamisega kaasnevaid võimalikke keskkonnamõjusid, sh. mõju C sidumisele. Hall-lepikud on olulised C-d siduvad ökosüsteemid ja neis talletatakse C valdavalt puude biomassis. Et C sidumine toimub intensiivsemalt nooremates ja keskealistes puistutes, siis on efektiivse C sidumise seisukohast hall-lepikute majandamisel oluline optimaalse raieringi rakendamine. Vanemates puistutes kasvukiirus väheneb, C sidumise intensiivsus langeb ning nad võivad muutuda C allikateks.

Samuti on optimaalse raieringi rakendamine efektiivse C sidumise seisukohalt oluline kõdusookaasikute majandamisel. Kuna C sidumine oli ka nende puhul kõrge noortes puistutes, aga vana (78 a.) sookaasik oli C-d emiteeriv metsaökosüsteem, siis ka selliste metsade puhul aitab optimaalse raieringi rakendamine suurendada C sidumise efektiivsust. Veelgi enam, kuna sookask on oma olemuselt aeglasekasvuline puuliik, siis sookaasiku asendamine järgmises põlvkonnas produktiivsema metsaga (kuusik, sanglepik) aitab samuti kaasa suuremale C sidumisele,

mis parandaks ühtlasi ka metsade majanduslikku väärtust. Kuusikute puhul peab muidugi silmas pidama, et nad on turvasmuldadel eriti tormikartlikud.

See et harvendusraied suurendavad arukaasikute kvaliteeti ja summaarset produktsiooni, on üldine metsakasvatuslik teadmine. Käesolev uurimus näitas, et raiejärgne puude juurdekasvu kiirenemisele võib lisaks vähenenud konkurentsile kaasa aidata ka suurenenud omastatava lämmastiku (N) sisaldus mullas. Kuid vaatamata suurenenud mineraalse N sisaldusele mullas, ei suurendanud harvendamine N leostumist, st. ei põhjustanud N kadu ökosüsteemist.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my supervisor Professor Veiko Uri. His knowledge and commitment in supervising me in my studies and articles was invaluable. I thank him for having endless patience to deal with all the trouble that came along with the task of supervising my PhD studies.

This thesis would not have existed without the self-sacrificing biomass team, the main core consists of Jürgen, Mats, Hardo and Kristiina. Also, I am grateful to all students, who have been part of the team alongside their bachelors or masters studies, for without their help in the field and laboratory the data would be insufficient.

I thank my co-authors for their indispensable contribution to the articles. Without the special skills of the co-authors my research papers would have lacked in quality.

I am also grateful to Mrs Ester Jaigma for revising the English text of the thesis as well as my original papers.

A special gratitude goes to my parents, who have been supporting me throughout my studies, however they could. The main reason I did not quit my PhD studies, although everything seemed meaningless were my children Gregor, Mirtel and Trevor. You have given me the strength to carry on, no matter what.

The studies included in this thesis were financially supported by the Institutional Research Funding IUT21-04 of the Estonian Ministry of Education and Research as well as by the Environmental Investment Centre projects No 5725 "The effect of drainage to carbon budget of birch stands growing on organic soils" and No 11660 "Carbon budget in Scots pine chronosequence stands" and by the project of the Estonian Forest Management Centre No 1-18/271 "Effect of clearcut and thinning on forest carbon cycling". Also the research project No 1-18/113 "Carbon and nitrogen cycle in drained forests" (2013–2016), on the basis of which the current study was completed, was supported by the State Forest Management Centre of Estonia, as well as by the KAUR project "Monitoring and modelling of forest litter in Estonia (2014–2018).

I

ORIGINAL PUBLICATIONS

Morozov, G., Aosaar J., Varik, M., Becker, H., Lõhmus, K., Padari, A., Aun, K., Uri, V. (2019). Long-term dynamics of leaf and root decomposition and nitrogen release in a grey alder (*Alnus incana* (L.) Moench) and silver birch (*Betula pendula* Roth.) stands. Scandinavian Journal of Forest Research, 34(1): 12-25.

Scandinavian Journal of Forest Research

ISSN: 0282-7581 (Print) 1651-1891 (Online) Journal homepage: http://www.tandfonline.com/loi/sfor20

Long-term dynamics of leaf and root decomposition and nitrogen release in a grey alder (*Alnus incana* (L.) Moench) and silver birch (*Betula pendula* Roth.) stands

Gunnar Morozov, Jürgen Aosaar, Mats Varik, Hardo Becker, Krista Lõhmus, Allar Padari, Kristiina Aun & Veiko Uri

To cite this article: Gunnar Morozov, Jürgen Aosaar, Mats Varik, Hardo Becker, Krista Lõhmus, Allar Padari, Kristiina Aun & Veiko Uri (2018): Long-term dynamics of leaf and root decomposition and nitrogen release in a grey alder (*Alnus incana* (L.) Moench) and silver birch (*Betula pendula* Roth.) stands, Scandinavian Journal of Forest Research, DOI: 10.1080/02827581.2018.1521468

To link to this article: https://doi.org/10.1080/02827581.2018.1521468

Published online: 22 Sep 2018.

SCANDINAVIAN JOURNAL OF FOREST RESEARCH
https://doi.org/10.1080/02827581.2018.1521468

Taylor & Francis
Taylor & Francis Group

Long-term dynamics of leaf and root decomposition and nitrogen release in a grey alder (*Alnus incana* (L.) Moench) and silver birch (*Betula pendula* Roth.) stands

Gunnar Morozov [a], Jürgen Aosaar [a], Mats Varik [a], Hardo Becker [a], Krista Lõhmus[b], Allar Padari[a], Kristiina Aun[a] and Veiko Uri[a]

[a]Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Tartu, Estonia; [b]Faculty of Science and Technology, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

ABSTRACT

The decomposition of the leaf litter, fine roots ($d < 2$ mm) and coarser roots ($2 \leq d < 5$ mm) of grey alder and silver birch, as well as of α-cellulose sheets using the litterbag method was studied in two experimental stands on Podzoluvisol soils in Southern Estonia. For both tree species, the coarser roots decomposed faster than the fine roots, ($p < .05$), tree species did not affect the decomposition rate of the roots ($p > .5$). The nitrogen (N) input to soil from aboveground litter was multiple times higher than the N flux from roots. The remaining relative ash-free mass of the leaves of grey alder and silver birch after three and a half years was similar. After 11 years the remaining relative ash-free mass of the fine and coarser roots of grey alder still accounted for around 10% of the initial value. For silver birch the remaining value was around 20% after 9 years. The litterbag method to underestimates in fertile soils the decomposition of organic matter and thus did not reflect the actual dynamics of decomposition.

ARTICLE HISTORY
Received 15 February 2018
Accepted 3 September 2018

KEYWORDS
Leaf litter decomposition; fine root decomposition; litterbag method; nitrogen dynamics; silver birch; grey alder; carbon

Introduction

From the point of view of carbon (C) cycling in forest ecosystems, decomposition of organic matter plays an important role since the input of fresh organic C into the soil is a major factor contributing to C accumulation in the soil, as well as to the soil heterotrophic respiration flux. In recent decades efforts have been made to clarify the role of forests in global and regional C sequestration (Dixon et al. 1994; Peng et al. 2008; Grüneberg et al. 2014; Krueger et al. 2017). Globally the carbon (C) stock in forests is divided between soil (44%), live biomass (42%), deadwood (8%) and litter (5%); in boreal forests the deposition of C in biomass is 20% and in soil 60% (Pan et al. 2011). Hence studies of C budgets on the ecosystems scale are crucial for understanding the driving forces of the functioning of the C cycle and C sequestration capacity (Fang et al. 2007); in this aspect, the plant litter decomposition process is a one key factor.

Decomposition of organic matter is an important process also for ensuring nutrient cycling in various forest types and is strongly related to ecosystem production. In some terrestrial ecosystems, more than 90% of net aboveground primary production may return to the soil in the form of litter proving a major resource for soil decomposers (Swift et al. 1979). Thus, both above- and belowground plant litters, are a main nutrient source for soil microorganisms (Persson 1979; Persson et al. 1980; Berg 1986) and may cover an essential part of the annual nitrogen (N) demand of deciduous stands (Uri et al. 2011; Aosaar et al. 2016). However, the share of the aboveground and belowground litter fluxes may vary to a large degree; the input of organic matter and N from dead fine roots into the soil may even exceed the amount of aboveground litter introduced to the soil (Persson 1978; Vogt et al. 1986). On the other hand, the input of aboveground litter in the soil may sometimes be significantly larger than the input of organic matter from fine roots (Uri et al. 2011, 2017a; Varik et al. 2015). When there is a number of studies on leaf and twig litter decomposition (Bocock 1963; Berg et al. 1982; Meentemeyer and Berg 1986; Chamier 1987; Šlapokas and Granhall 1991a, 1991b; Dilly and Munch 1996, *etc.*), then studies on root decomposition are scarce (Berg 1984; Lõhmus and Ivask 1995; Palviainen et al. 2004; Püttsepp et al. 2007). Studies focusing on decomposition of both leaf litter and fine root litter in a complex manner have been unavailable.

Decomposition of plant litter is a complex process which involves leaching, breaking up by the soil fauna, transformation of organic matter by micro-organisms and transferring of organic and mineral compounds to the soil. There are several factors affecting decomposition of forest litter, among them temperature, moisture, tree species, slope position, litter supply, understorey vegetation, acidity, soil properties and biological activity, and especially the soil microfauna (Berg and Staaf 1981; McClaugherty and Berg 1987; Šlapokas and Granhall 1991a; Lavelle et al. 1993; Kavvadias et al. 2001). Some authors (Ormerod et al. 1993) have found human activity to be also a factor in forest litter decomposition. All these circumstances make it difficult to develop general decomposition models for different forest ecosystems.

CONTACT Gunnar Morozov gunnar.morozov@emu.ee Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, F. R. Kreutzwaldi 5, Tartu 51006, Estonia

Both grey alder (*Alnus incana* (L.) Moench) and silver birch (*Betula pendula* Roth) are widespread and very common deciduous pioneer tree species in the Nordic and Baltic countries. Birch and grey alder dominated forest land area, making up 29.5 and 9.0%, respectively, of all forest land in Estonia (Yearbook 2016). Grey alder has a great potential as a promising fast-growing tree species for short-rotation forestry (Rytter 1996; Uri et al. 2002, 2011, 2014; Hytönen and Saarsalmi 2009; Aosaar et al. 2012, 2013; Rytter and Rytter 2016). However, since alder species are N fixing (Bonan 2008; Granhall 1994) and symbiotically fixed N reaches the soil mainly through leaf litter (Rytter 1990; Uri et al. 2011), the decomposition process of N rich leaf and root litter (Lõhmus et al. 2002) may be quite intensive. The average concentration of N in grey alder leaf litter is high due to low autumn retranslocation flux and estimated roughly over 3% (Uri et al. 2002, 2011). Silver birch is the most important broad-leaved tree species in Estonian forestry; it has a wide natural distribution area on the Eurasian continent, ranging from the Atlantic to Eastern Siberia. Although silver birch occurs almost throughout the whole of Europe, the most abundant birch resources are located in the boreal and temperate forests of Northern Europe, where birches are the most important commercial broad-leaved tree species (Hynynen et al. 2010). For silver birch higher N retranslocation from senescent leaves (55-60%) is inherent and thus N content of leaf litter is lower (ranging between 1-1.5%) (Uri et al. 2007; Aosaar et al. 2016) compared to grey alder.

Despite their relatively small biomass (Keyes and Grier 1981, Vogt et al. 1996), the fine roots have an enormous surface area, growing and turning over rapidly (Rytter 2013), which is important in terms of substance cycling and energy flow in forest ecosystems (Zhou and Shangguan 2007). Thus the fine roots are essential for their contribution to C cycling in forest ecosystems (Brunner and Godbold 2007). Studies (Persson 1983; Vogt et al. 1983; Brunner et al. 2013) have shown that the production and replacement of fine roots may form a big part of net primary production (NEP) in boreal forest. However, from the methodological viewpoint, estimation of the nutrient or C input in the soil via decomposition of root litter is more sophisticated since roots are continuously growing and dying, making it hard to partition the decomposition process.

The objective of this study was to estimate the decomposition dynamics of leaf litter and fine roots as well as coarser roots in young grey alder and silver birch stands, growing on fertile soil on abandoned agricultural land and increase our understanding of the root and leaf litter decomposition process in soil. The specific objective was to evaluate and review the suitability of the litterbag method as a way to describe the rate of decomposition of plant litter.

The hypothesis of this study was that in similar soil conditions both the leaf litter and root litter of grey alder decompose more intensively, compared to the leaf and root litter of birch, because of their higher nitrogen content and a more favourable C:N ratio.

Material and methods

Description of the study sites

Both leaf and root litter decomposition experiments were carried out at two sites – a young grey alder stand and a young silver birch stand (Table 1). The stands were similar regarding land use history, both growing on abandoned agricultural land as first generation forests. The grey alder stand is

Table 1. Main stand characteristics for the studied sites at the beginning of a particular experiment. The soil characteristics represent upper 0–10 cm soil layer. The characteristics of the grey alder stand are presented in Uri et al. (2002, 2009) and the characteristics of the silver birch stand are presented in Uri et al. (2007, 2008).

	Grey alder (58° 3′ N 27° 12′ E)		Silver birch (58° 14′ N 26° 44′ E)
	Leaf decomposition	Root decomposition	Leaf and root decomposition
Substrate information	80 bags of leaves; (1.7–2.8 g) 40 bags of cellulose in top soil layer; (1 ± 0.1 g) 40 bags of cellulose on soil surface; (1 ± 0.1 g)	80 bags of fine roots; (1 ± 0.1 g) 80 bags of coarser roots; (1 ± 0.1 g)	80 bags of leaves; (2.0–2.1 g) 80 bags of fine roots; (1 ± 0.1 g) 80 bags of coarser roots; (1 ± 0.1 g)
Beginning of experiment	Leaves, cellulose; November 1996	Roots; August 2002	Leaves, roots; November 2004
End of experiment	Leaves; June 2000 Cellulose in top soil layer; September 1997 Cellulose on soil surface; September 1998	Roots; October 2013	Leaves; May 2008 Roots; November 2013
Stand characteristics			
Age of stand, yr	3	9	8
Average stand height, m	2.1	8.5	6.6
Average stand $D_{1.3}$, cm	–	5.2	3.2
Basal area m^2 ha^{-1}	–	17.8	8.6
Number of trees per ha	14,020	8400	11,600
Soil characteristics			
Soil type	Eutric Podzoluvisol		Glossic Podzoluvisol
N, mg kg^{-1}	1030	1270	950
Organic matter content, %	2.81	2.97	2.32
Available P, mg kg^{-1}	56.98	53.50	71.98
Available K, mg kg^{-1}	170.34	178.34	210.24
pH_{KCl}	5.73	5.02	5.60
C:N ratio	16	14	14
Bulk density (g cm^{-3})	1.28	1.28	1.34

located in the south-eastern part of Estonia, and was planted in 1995. The plantation was established on an abandoned farmland and one-year-old plants of natural origin were used. The area of the stand was 0.08 ha and it had not been used as an active farmland for 2 years before planting (Uri et al. 2002). The initial density of the stand was 15,750 trees per hectare. There had not been done any weed control, fertilization or other treatment on the stand (Uri et al. 2009). A more detailed description of its establishment and initial growth is published in several earlier studies (Uri et al. 2002, 2009, 2011).

The naturally regenerated silver birch stand was also located in the south-eastern part of Estonia, in Tartu county. At the time of the beginning of the experiment (2004), the stand was 8 years old (Table 1). The soil type was similar to that of the grey alder experimental stand. A more detailed description of its establishment and initial growth is published in earlier studies (Uri et al. 2007; Aosaar et al. 2016).

As the distance between the two stands is roughly only 35 km, climatic conditions in both stands can be regarded as similar. The mean annual temperature at both sites is 6 °C, the mean precipitation is 653 mm and the mean length of the vegetation period (daily average temperature exceeds +5°C) is 191 days (Aosaar et al. 2013). According to the data from the Võru station of the Estonian Weather Service (2017) for the period between 1996 and 2013, precipitation varied from 462 to 898 mm and the length of the vegetation period varied from 169 to 217 days (Appendix 1).

Installation of the experiments

Leaf litter and cellulose

For both grey alder and silver birch, a similar experimental design was used. The leaves for incubation were collected in the same year when the experiment was initiated from litter traps of the same stands and dried in a laboratory oven at +70°C to a constant weight. Dried leaf litter was then divided into 80 individual samples (for both species) with a weight ranging from 1.7 to 2.8 grams for grey alder and from 2.0 to 2.1 grams for silver birch and were placed into 15 × 15 cm litterbags made of 1 mm polypropylene mesh. Each individual sample was weighed to 0.01 g and a plastic label with the number of the sample was inserted into a litterbag for further identification of the sample. Altogether 80 leaf litterbags were divided between 8 strings, with 10 litterbags each.

The strings were randomly placed in the studied stand and marked. The vegetation residue was removed from soil surface so that the bags were in contact with the mineral soil. The experiment with leaf litter was initiated in November 1996 for grey alder and in October 2004 for silver birch (Table 1).

In the grey alder stand, besides leaves, also sheets of cellulose were simultaneously incubated at the same site. The cellulose decomposition experiment allowed to estimate the activity of decomposers in relation to the decomposition rate of cellulose, which is an important component of plant fractions. For the cellulose study, sheets (dimensions 3 × 5 cm) with a weight of 1 ± 0.1 g were used. Cellulose consisted of 95% of α-cellulose and 5% of β- and γ-cellulose. All substrates used in this study were dried to an air dry state and weighed before placing them into the litterbags for the experiment. The pieces of cellulose, altogether 40 samples, were incubated on soil surface and in the top soil layer (A horizon) to a depth of approximately 5 cm. All samples were incubated in similar polypropylene mesh bags with 1 mm mesh. The experiment was launched in November 1996 and the first collection of samples took place after 16 weeks, in March 1997.

In autumn 2004, the leaf litter decomposition experiment was established at the silver birch study site. The method of collecting and processing leaves was similar to that employed in the grey alder experiment.

Fine and coarser roots

The decomposition experiment with the fine ($d < 2$ mm) and coarser roots ($2 \leq d < 5$ mm) of grey alder was initiated in August 2002. Silver birch roots were incubated in November 2004, simultaneously with the leaf litter decomposition experiment. The roots for the experiments were collected in the summer of the same year and from the same stands using a spade for taking soil samples from a depth of up to 20 cm. The roots were separated and gently washed in tap water to remove adhering soil particles. The roots were then divided into different fractions (fine roots $d < 2$ mm and coarser roots ($2 \leq d < 5$ mm) in the laboratory. The roots that were dead or decaying as well as the roots of the understorey vegetation were removed. Only the roots that seemed alive at the time of collecting were stored for further experiment. The roots were dried to an air dry state at 70°C, hacked into approximately 1 cm pieces and placed in nylon fabric litterbags with dimensions of 5 × 5 cm and with a mesh size of 0.14 mm. The weight of the roots in every bag was set exactly at 1.000 g. Five samples from every fraction were separated for initial chemical analyses as well for estimation of ash content. The samples were incubated in the soil at a depth of 5–10 cm.

In the grey alder experiment there were altogether 4 transects, each transect had two rows, with 20 litterbags attached to each. In the silver birch experiment there were 5 transects, each transect had two strings, with 16 litterbags attached to each (one row with $d < 2$ mm and the other with $2 < d <$ 5 mm roots). In total 160 bags with roots (80 of $d < 2$ mm and 80 of $2 < d < 5$ mm) were buried in the experimental area for both tree species.

Collecting and processing of the samples

Leaf litter and cellulose samples

In the grey alder stand the litterbags with leaf litter were collected between July 1997 and June 2000. During four years collecting dates were July 1997, September 1997, October 1997, May 1998, July 1998, October 1998, June 1999 and, June 2000.

The litterbags with silver birch leaf litter were sampled between June 2005 and May 2008. During four years the collecting dates were June 2005, July 2005, August 2005,

September 2005, May 2006, August 2006, October 2006, November 2007, and May 2008.

For every leaf litter sampling, on average 9 (range 8–16) samples from either experiment were collected. The collected samples were transported to the laboratory, the bags were cut open and leaf litter or cellulose residues were carefully separated. The leaf pieces were cleaned with a small brush, oven dried to constant mass at 70°C and weighed to 0.001 g; next, mass loss was calculated. Also the samples were analysed for ash content and nitrogen concentration. The remaining dry weight was corrected by taking ash content into account.

Root samples

The bags with grey alder roots were first collected in October 2002. During the next eleven years, the bags were collected irregularly. The collecting dates were October 2002, May 2003, August 2003, October 2003, October 2004, October 2006, October 2009, October 2010, and the last batch of bags was collected in October 2013.

The collection of litterbags with silver birch roots started in August 2005. The period during which the sample bags were collected lasted 9 years, the final batch of bags was collected in November 2013. Altogether the samples were collected in six lots. The dates of collection were: August 2005, October 2005, August 2006, October 2006, October 2009, October 2010, and November 2013.

The procedure for sample collection was similar to that followed in the leaf litter decomposition experiment. Each sample was cleaned from adhering soil particles and fresh roots that had penetrated the bags were extracted. The cleaned samples were dried at 70°C during two days and dry weight was determined. For every sampling, on average six (range 5–16) samples from $d < 2$ mm and $2 < d < 5$ mm were taken.

The relative remaining mass of the decomposed samples both for leaf litter as well as for the root samples was calculated based on differences in litter mass for a particular sampling time and the initial mass of the samples. The weight of the samples was corrected with a coefficient for mass to correspond with ash content.

The remaining ash free mass of the decomposed leaves and roots was described by an exponential function (1).

$$M_t/M_0 = e^{-k(t)\cdot t}, \quad (1)$$

where $k(t) = a{\cdot}c{\cdot}t^{-b}$, a, b – coefficients, c – ANOVA coefficient, t – time in weeks, M_0 – ash free dry mass of the initial samples, M_t – ash free dry mass of the sample at time t.

For regression analysis, function 1 was transformed to have the following form:

$$\ln(-\ln(M_t/M_0)/t) = \ln(a) + \ln(c) + b \cdot \ln t. \quad (2)$$

The remaining ash free mass of decomposed cellulose in the soil was described by a linear function (3).

$$k(t) = -a \cdot t + b, \quad (3)$$

where k – rate of decomposition, i.e. the ratio of the remaining mass of the substrate (after a certain time of decomposition) to the initial mass of the substrate.

Litter input flux to soil

Taking into account the annual above ground and below ground litter input to soil in both studied stands which were estimated in our earlier studies (Uri et al. 2007, 2009, 2011; Aosaar et al. 2013, 2016) we calculated the annual N release to soil from decomposed litter.

Laboratory analysis

The leaf and root samples were analysed for total Kjeldahl nitrogen, total Kjeldahl phosphorus, potassium and ash concentration. The block digestion and steam distillation methods were used for testing the plant material for nitrogen concentration (Tecator AN 300). Digest by flow injection analysis was performed for testing the plant material for Kjeldahl phosphorus concentration (Tecator AN 5242) using the analyser Fiastar 5000. To test the plant material for potassium, the flame photometric method was employed. For AD cellulose and AD lignin analyses the forage fibre technique was used with the equipment and methods by Tecator (AN 304, ASN 3436, ASN 3430). The fractions of AD fibre and AD lignin were determined successively by using sulphuric acid (AOAC method no. 973.18, 1990) and by calculating AD cellulose as AD fibre – AD lignin. For testing N (Kjeldahl) in the soil samples, Tecator ASN 3313 was implemented. Available phosphorus (ammonium lactate extractable) in the soil was determined by flow injection analysis with the use of Tecator ASTN 9/84. Available potassium was determined from the same solution by the flame photometric method. Magnesium in the soil was determined by flow injection analysis with the use of Tecator ASTN 90/92.

The analyses were performed at the Biochemistry Laboratory of the Estonian University of Life Sciences.

Data analysis

Normality of variables was determined by Lilliefors' and Shapiro-Wilk's tests. The t-test for independent samples by groups was employed to compare the decomposition rates of the different substrates.

For comparing the decomposition dynamics of different tree species or root fractions, ANOVA was used.

The regression models were used for describing the dynamics of decomposition of the incubated samples. Linear and exponential models were employed for estimating relationships. The measure of the fit of the models was based on the coefficient of determination (R^2) and the level of probability (p). In all cases the level of significance α=0.05 was accepted. The softwares STATISTICA 13.0 and R (Crawley 2007) were employed.

Results

Leaf litter and cellulose

For both studied species, an exponential function (1) described decomposition rate during the four study years (Figure 1; Table 2).

The mass losses of leaf litter for both silver birch and grey alder followed a similar pattern: during the first 12 months the loss of mass from the initial value was significant, at 57% and

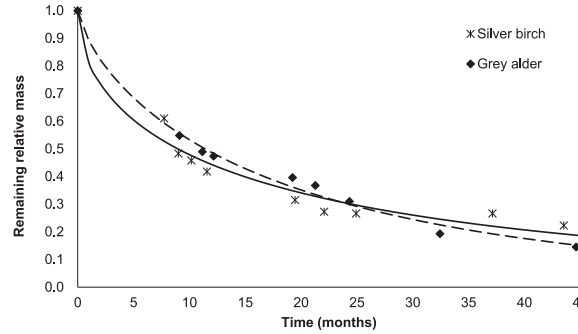


Figure 1. The dynamics of remaining relative dry mass of silver birch and grey alder leaf decomposition over 3 years of the experiment ($N = 160$).

53%, respectively (Figure 1) and decreased sharply thereafter. However, the leaves of silver birch tended to lose their mass faster in the first year, compared to grey alder leaves. The rate of decomposition in the second year was similar for both grey alder (16% of remaining mass) and silver birch leaves (14%). Three years after the installation of the experiment approximately 20% of the initial leaf mass was still left for both species. At the end of the experiments (after 44 and 45 months) the remaining relative mass of the silver birch and grey alder leaves was 19% and 15%, respectively. There was a trend according to which silver birch leaves lost more relative mass compared to the grey alder leaves, then later on the mass of the silver birch leaves decreased more slowly than the mass of the grey alder leaves.

However, since the lines of the functions describing the dynamics of decomposition crossed, we could not apply ANOVA for testing the statistical difference as we did in the case of roots (ch. 3.2.).

The initial nitrogen (N) concentration of the incubated leaves was lower in the silver birch samples (Figure 2 and Table 3) and throughout the experiment the concentration of N in the silver birch leaves remained lower compared to the grey alder leaves. However, the dynamics of N concentration was similar for both species: it increased during the first 20 months and started to decline thereafter (Figure 2). The decline lasted till month 25 for silver birch and month 32 for grey alder, after that a slight increase of the concentration was demonstrated again.

In the soil, the decomposition of cellulose was very fast; after 32 weeks only about 20% of the initial mass was left and after 41 weeks cellulose had almost disappeared from the litterbags. Since the samples were incubated in late autumn (November), intensive decomposition started in spring and the subsequent mass loss of the samples was described by a linear model (Figure 3). The samples which were incubated on soil surface had lost less than 10% of the initial mass after 45 weeks of decomposition. As late as 75 weeks after incubation, the decomposition process intensified and by the end of the second year practically all cellulose on top of the soil had decomposed. In the second year the decomposition rate of cellulose on soil surface was similar to that of cellulose in the soil in the first year. When comparing the two experiments the overall rate of decomposition was almost double in the samples incubated in the soil.

At the beginning of the experiment, nitrogen (N) was absent from the cellulose substrate; at the first sampling after 7 months of decomposition N was present in the incubated cellulose sheets both in the soil and on soil surface (Table 4). However, the increase was 7 times larger in the samples inserted in the soil, reflecting the higher abundance of decomposers there. After almost a year of decomposition there was far more N in the cellulose pieces decomposing in the soil compared to the cellulose decomposing on soil surface. The decomposing cellulose sheets demonstrated an increase of N concentration at the earlier stage of decomposition and a decrease at a later stage.

Table 2. Parameter estimates of function (1) for estimation of the decomposition dynamics of grey alder and silver birch leaf and root litter.

Substrate		a	b	R^2
Silver birch leaves		0.2857	0.548	0.948
Grey alder leaves		0.1163	0.267	0.827
Grey alder roots	<2 mm	0.0523	0.279	0.766
	2–5 mm	0.0888	0.370	0.892
Silver birch roots	<2 mm	0.0898	0.417	0.904
	2–5 mm	0.1458	0.511	0.951

Root litter

The two grey alder root fractions had a similar decomposition pattern which can be characterized by an exponential function (1); the function parameters for the different root fractions are presented in Table 2.

After 64 weeks of decomposition, the remaining initial mass of the fine roots and coarser roots accounted for 64% and 57% of the initial value, respectively (Figure 4), thereafter the decomposition process slowed down. Roughly 11 years from the beginning of the experiment, the remaining mass of the fine roots and coarser roots made up still 11% and 9% of the initial value, respectively and the decomposed material was still recognized as roots.

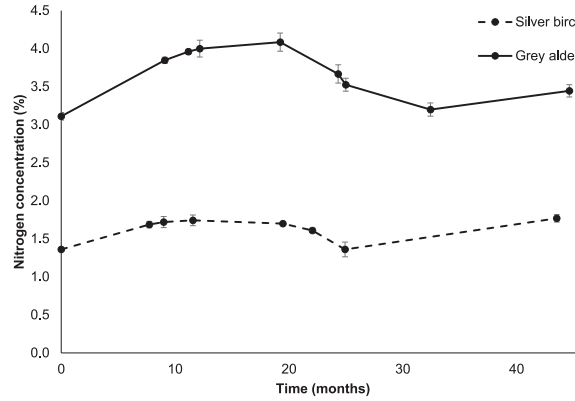


Figure 2. The dynamics of nitrogen concentration in decomposing grey alder ($N = 9 \times 5$) and silver birch ($N = 8 \times 5$) leaf litter. Bars indicate standard error.

For comparing the decomposition dynamics of the different fractions, ANOVA was used. On the basis of equation (2) parameter ln(*c*) was calculated to be −0.2409 (Appendix 2). Although the pattern of mass decrease was similar for both fractions, their decomposition rates were statistically different (p-value for the parameter ln(*c*) is 0,045): the fine roots ($d < 2$ mm) lost their initial mass more slowly compared to the coarser roots ($2 < d < 5$ mm) (Figure 4) (pairwise *t*-test, $p < .01$).

For clarifying the effect of root diameter on decomposition rate in silver birch, the same approach, i.e. a regression model (1) (Table 2), was used.

By using equation (2), ANOVA parameter ln(*c*) was calculated to be −0.1571 with p-value .093. Root diameter was an insignificant factor on the confidence level 95%, but significant on confidence level 90%. However the decomposition of the coarser root fraction was slightly faster (Figure 5, Appendix 2).

For both silver birch and grey alder, intensive loss of the initial mass occurred within 100 weeks of the experiment when the mass of the decomposed samples decreased roughly 50% for both fractions (Figures 4 and 5).

The biggest difference in the relative remaining mass between the two fractions for both studied tree species occurred after one year of the beginning of the experiment ($p = .0002$ and $p = .004$), respectively (Figures 4 and 5). Later on this difference decreased and levelled out by the end of the experiment ($p = .532$). At the end of the experiment, i.e. after roughly 9 years of decomposition, the remaining relative mass of the fine and coarser roots still accounted for 21 and 20% of the initial value, respectively.

For comparison of the decomposition of same root fraction for two different tree species (grey alder *versus* silver birch), ANOVA was applied (equation 2). ANOVA parameter ln(*c*) for the 2 mm roots was -0.0730 with *p*-value 0.54 and for the coarser roots −0.0161 with *p*-value 0.876 (Appendix 2).

Two last ANOVA analysis show that that tree species is insignificant factor for the decomposition of roots and thus the decomposition of both root fractions of silver birch and grey alder was similar.

Although the roots of grey alder had a higher concentration of N compared to the silver birch roots (Table 3 and Table 5), a similar trend for fine roots was revealed for both species: N concentration increased in the earlier stages of the decomposition process, reaching a peak somewhere in the middle of the experiment, and started to decrease slowly thereafter but still remaining higher compared to initial concentration. The trend for N concentration of coarser roots was a steady increase till the end of the experiment.

It is evident that the decomposition rate K is higher in the first phase of decomposition and decreases over time for birch roots (Figure 6). In the early phase the K values of fine ($d < 2$ mm) and coarser roots ($2 < d < 5$ mm) were greater and after a while the decomposition rate of both fractions was similar.

Table 3. Initial nutrient and ash content (%) in the incubated leaves and root samples; ($N = 6 \times 5$). N – Kjeldahl nitrogen, P – phosphorus, K – potassium, ±SE.

Fraction	N	P	K	C:N	Ash content	Cellulose %	Lignin %
Leaves of silver birch	1.36 ± 0.07	0.32 ± 0.01	1.16 ± 0.06	36.3	5.58 ± 0.18	41.2 ± 0.95	45.0 ± 2.21
Leaves of grey alder	3.11 ± 0.02	0.16 ± 0.01	1.20 ± 0.05	16.3	6.20 ± 0.20	36.7 ± 2.08	48.2 ± 0.83
Roots of silver birch ($d < 2$ mm)	0.70 ± 0.03	0.11 ± 0.01	0.20 ± 0.01	73.3	4.33 ± 0.49	38.7 ± 2.3	38.7 ± 0.00
Roots of silver birch ($2 \leq d < 5$ mm)	0.59 ± 0.01	0.14 ± 0.01	0.23 ± 0.01	84.1	3.64 ± 0.10	54.2 ± 0.35	29.4 ± 0.55
Roots of grey alder ($d < 2$ mm)	1.29 ± 0.05	0.18 ± 0.01	0.47 ± 0.01	39.7	5.25 ± 0.32	43.9 ± 1.21	35.3 ± 0.88
Roots of grey alder ($2 \leq d < 5$ mm)	1.05 ± 0.03	0.16 ± 0.01	0.48 ± 0.01	47.5	4.37 ± 0.35	59.5 ± 0.46	26.0 ± 0.78

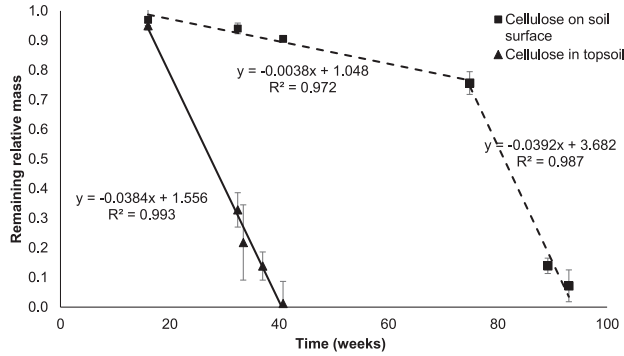


Figure 3. The dynamics of remaining relative mass of cellulose in the soil and on soil surface ($N = 80$), (mean ± SE).

In both stands main share of available N from decomposition of organic litter derived from leaf litter (Table 6) and the N input to soil from root litter was very modest.

Discussion

Decomposition of leaf litter and cellulose

The dynamics of leaf litter decomposition in current study was similar for both studied tree species, following a negative exponential function, being in good accordance with several earlier results (Slapokas and Granhall 1991a; Berg 2000; Vares 2001; Prescott 2010). During the first year of incubation, the decrease of the relative mass of leaf litter was intensive for both tree species, reaching roughly 60% of the initial mass and slowing down thereafter (Figure 1). According to Coûteaux et al. (1995) litter mass loss takes place in two phases – mineralization and humification of litter, and the leaching of soluble into the soil. The first one is faster and consist mainly of leaching, mineralization, and humification of easily obtainable matter for microorganisms; the following stages consist of mostly mineralization and humification of less obtainable compounds (lignin, hollocellulose). The huge amount of mass loss in the early phase of decomposition can be attributed to the leaching process, where watersoluble substances are carried out of litter, and to the degradation of free unshielded holocellulose (Berg 2000). In the last phase (from month 25 to month 45) the loss of relative mass was between 3% and 4% for both substrates.

Table 4. The dynamics of nitrogen (N) concentration (%) in the decomposed cellulose sheets, ($N = 8 \times 5$).

	Time, weeks				
	0	32	33	37	41
On soil surface	0 ± 0.00*	0.094 ± 0.01*		0.082 ± 0.06	0.077 ± 0.09
In the upper soil layer	0 ± 0.00*	0.693 ± 0.03*	0.448 ± 0.04*	0.283 ± 0.04*	

*Date of initiation of the experiment ($p < .05$).

Decomposition and mineralization of organic matter releases nutrients to plants, thereby ensuring preconditions for higher productivity of the ecosystem. On one hand, decomposition rate depends on the quality of organic matter generated by the trees (Lovett et al. 2004; Asplund et al. 2017) and reaching the soil; on the other hand, site fertility is also an essential factor. However, in the current study, soil nutrient content as well as the soil C:N ratio (14–16) remained in same magnitude for both studied stands (Table 1).

It was hypothesized that the leaf litter of grey alder decomposes faster because of its higher N content, but it was not proved in current study. It is well known that the N content and the C:N ratio of decomposing organic matter has a strong effect on decomposition (Slapokas, 1991b; Scott and Binkley 1997); high level of initial N increases decomposition rate (Maloney and Lamberti 1995; Dilly and Munch 1996; Horodecki and Jagodziński 2017). Low level of N hinders the decomposition process and nitrogen starts to accumulate in litter to reach a critical concentration of 1.4–1.7%, after which it will be released from decomposing litter (Waksman 1952; Ågren and Bosatta 1996). In our case initial N concentration in decomposing birch leaves was roughly 1.4% (Table 3) which responds to lower limit of above mentioned critical threshold. The initial N concentration in grey alder decomposing leaves was more than two folds higher from critical (Table 3) but dynamics of mass loss over 3 years of the experiment was similar for both species (Figure 1). Probably for effective decomposing is decisive exceeding critical value of N concentration in leaf litter and further increase of N does not affect decomposition process substantially. However, decomposition of plant litter is a complex process which influenced by several factors, among of them by concentrations of other nutrients as well as by content of cellulose and lignin. Mikola (1958) has stated that addition of plant litter, which is rich in cellulose or other carbohydrates and poor in N, to the soil reduces the production of plants as cellulose-decomposing microbes use up all available N. According to Berg (2000), the concentrations of major nutrients (N, P, S) in organic litter had a major effect in the early

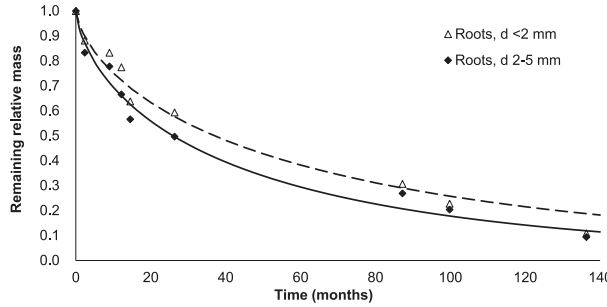


Figure 4. The dynamics of mass loss in the different grey alder root fractions during the 11-year decomposition period ($N = 160$).

stages of decomposition. On other hand, high level of lignin in the substrate may decrease the decomposition rate of litter (McClaugherty and Berg 1987; Camiré et al. 1991). In our study the content of lignin in grey alder leaf litter was higher than in birch litter (Table 3) which may increase mass loss of birch litter since cellulose decomposes faster than lignin. Also the nitrogen:lignin-ratio, the carbon:mineral element-ratio and the C:N-ratio have been found to affect decomposition rate (Howard and Howard 1974; Tian et al. 1992; Tripathi and Singh 1992). Tripathi et al. (2006) found the ratios of lignin:N and C:N to be negatively correlated with mass decrease rate at different stages of litter decomposition. The C:N ratio for the grey alder leaves used for decomposition experiment was 16 and for the silver birch leaves, 36 (Table 3). The high N concentration in the grey alder leaves and low C:N ratio is caused by the low autumn retranslocation of foliar N; and the leaf litter of alders is N rich (Rytter 1995; Saarsalmi 1995; Mander et al. 1995). Average resorption efficiency was 3–11% in the studied grey alder stand (Uri et al. 2011) and between 55 and 60% in the silver birch stand (Uri et al. 2007; Aosaar et al. 2016). Despite a significant difference in the quality of the decomposing substrate in terms of N content, the dynamics of mass loss was similar for both species ($p > .05$) (Figure 1).

We compared the decomposition dynamics of grey alder and silver birch leaf litter, however, the shortcoming is that these experiments were carried out in different periods (Table 1). It is evident that among the various other factors also weather conditions played a role in decomposition dynamics. Especially at the beginning of the experiments the weather conditions have a greater impact since a large mass loss occurs in the first phase of the decomposing experiment. Still, this effect was quite weak since there were no extreme weather events during either period (Appendix 1). As the experiments lasted for more than one individual year (for leaves over 3 years and for roots of silver birch and grey alder 9 and 11 years, respectively) allowed to suppose that possible weather extremes levelled during so long period.

The decomposition experiment with cellulose sheets was included in the study since cellulose decomposition indicates potential soil fertility and soil microbial activity. However, the active microbial biomass, determined by substrate-induced respiration (SIR) and microbial respiration activity (BAS) for the studied alder stand in 1999, (6-year-old stand) were relatively low (0.24 mg C g^{-1} and 0.04 mg CO_2 g^{-1}) (Lõhmus et al. 2006). As expected, α-cellulose decomposition in the soil was very rapid: slightly over half of the initial mass was lost after half a year of decomposition (Figure 3). Since the

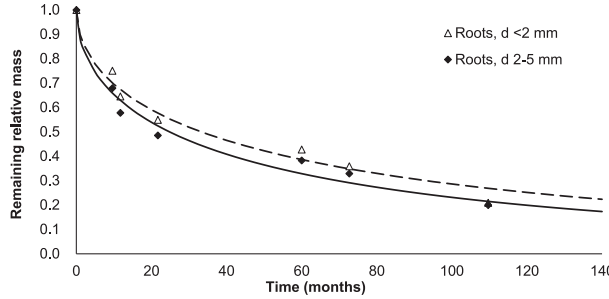


Figure 5. The dynamics of the remaining relative mass of the two silver birch root fractions during the 9-year decomposition process ($N = 160$).

Table 5. The dynamics of nitrogen concentration (%) in the fine root and coarser root fractions during decomposition ($N = 16 \times 5$), ±SE.

		Time, weeks							
Tree species	Fraction	0	10	38	50	113	312	374	428
Grey alder	<2mm	1.29 ± 0.05	1.43 ± 0.04	1.49 ± 0.05		1.98 ± 0.05		1.51 ± 0.09	1.39 ± 0.11
	2–5 mm	1.05 ± 0.03	1.15 ± 0.06	1.29 ± 0.01					1.56 ± 0.13
Silver birch	<2mm	0.7 ± 0.03			1.15 ± 0.05		1.10 ± 0.08		
	2–5 mm	0.59 ± 0.02			0.99 ± 0.01		1.15 ± 0.07		

studied grey alder stand is growing on former agricultural land, this may also be partly ascribed to the effect of previous land use. The first cellulose samples were collected immediately after winter (in March) and the mass of incubated cellulose was almost unchanged. We assumed that in winter, with frozen soil, decomposition had ceased and we used a negative linear function for describing the mass loss of cellulose samples (Figure 3).

The decomposition of the cellulose samples on soil surface had been slower, one year after incubation about 80% of the initial mass was left. Later on the situation changed: cellulose started to decompose rapidly and after two years of decomposing only 7% of the initial mass was left. The reasons for such an abrupt change in the decomposition rate can be manifold, e.g. favourable weather conditions, contact with the soil and tree litter, and presence and activity of decomposers. In the first year, the decomposition of cellulose on soil surface was most probably inhibited by the low abundance of decomposers. Because of poor contact with the soil, there occurred a lag phase. In the second year of the decomposition experiment with cellulose on soil surface the decomposition dynamics was similar to the dynamics of cellulose decomposition in the soil in the first year. The dynamics and rate of cellulose decomposition are affected by certain decomposers (Swift et al. 1979). If in the first phase of decay the content of N in the decomposing material is controlling the mass loss rate, in the later phases the content of cellulose and lignin will be increasingly more responsible for the rate of decomposition (Berg 1984; Taylor et al. 1989). We partitioned the decomposition of cellulose on soil surface into two phases and different negative linear models were the best to describe its dynamics in both cases (Figure 3).

The decomposition pattern of the cellulose samples in this study differs from that found by Püttsepp et al. (2007) in a willow plantation on abandoned agricultural land. In our study cellulose decomposed almost completely in 41 weeks while in the study of Püttsepp 35.9% of initial cellulose was left even after 51 weeks. However, in both studies the dynamics of decomposition was best described by a negative linear model.

Table 6. Annual leaf litter and root litter input to soil and cumulative nitrogen release dynamics for grey alder (10–12 years old) and silver birch stand (8–10 years old).

				Cumulative N release, kg ha^{-1}		
Stand	Litter type	Litter input, kg ha^{-1}	N input kg ha^{-1}	1. year	2. year	3. year
Grey alder	Leaf litter	3040	94.6	48.30	66.00	75.70
	Root litter	530	6.6	1.78	2.67	3.30
Silver birch	Leaf litter	3500	47.6	27.83	33.29	36.36
	Root litter	890	6.4	2.04	2.79	3.31

Root litter

Both studied species (grey alder and silver birch) had a similar decomposition pattern of roots of different diameters (fine roots $d < 2$ mm and coarser $2 \leq d < 5$ mm roots) (Figures 4 and 5). However, in both cases, the fine roots lost their initial mass more slowly than the coarser roots. This can be explained by the early loss of cortical material, which is easily degraded and would be more abundant in roots of larger diameter. Similar results were obtained also in a fine root decomposition experiment on Norway spruce (Lõhmus and Ivask 1995) where the roots with $d < 1$ mm maintained their relative initial mass better than the roots with $d <$ 2 mm. A number of other root decomposition studies have shown similar results (McClaugherty et al. 1984; Fan and Guo 2010, Goebel et al. 2011; Sun et al 2013; Xiong et al. 2013; Sun et al. 2016).

Intensive mass loss of decomposing fine roots in the first year is a typical pattern (Lõhmus and Ivask 1995; Püttsepp et al. 2007). After one year the remaining ash free weight of the fine roots ($d < 2$ mm) in the grey alder and silver birch stands made up 77% and 65% of the initial weight, respectively, which is less than reported in an earlier study (Püttsepp et al. 2007) for short rotation willow species ($d <$ 1 mm). However, the decomposition of roots was markedly slower than that of leaf litter. It is noteworthy that even after the ten-year decomposition period some root residuals had remained in the litterbags. This shows that decomposition of roots is a much slower process, which can be explained by several factors, among them lower nitrogen content of roots, especially silver birch roots (Table 3).

As found by Palviainen and Finér (2015), a higher lignin and lower carbohydrate concentration and also higher C:N ratio may be a reason for a slower decomposition rate of roots. In our study fine roots did have a higher lignin and ash content, and lower cellulose concentration (Table 3). The C:N ratio was higher in coarser roots; nevertheless, a favourable environment for decomposers was provided by a high N level in soil of two studied stands (Table 1). As noted above, higher lignin concentration suppresses decomposition of organic matter, whereas a high cellulose concentration promotes a faster decomposition. As roots grow in an aggressive environment, there exist several defense mechanisms (including changes in biochemical composition) against root pathogens. Fine roots with primary structure include fungal mycorrhizas and actinorrhizas, etc. According to Sun et al. (2016) a reason for the slow decomposition of finest roots may be higher concentrations of acid-unhydrolyzable fraction and a lack of secondary (wood) development, e.g. secondary xylem.

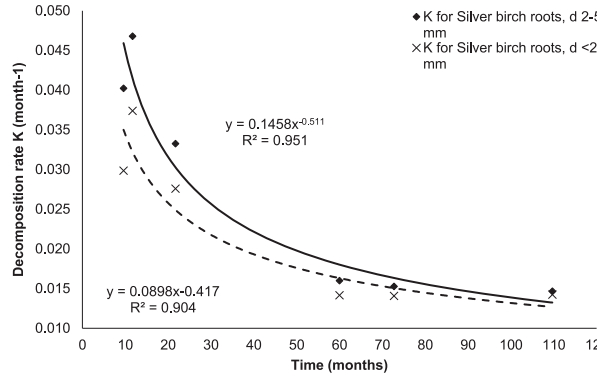


Figure 6. The dynamics of the decomposition rate *K* in the two fractions of silver birch roots during 9 years.

Considering that different functional groups of decomposers, e.g. microbes, bacteria and fungi, have the greatest impact on root decomposition rate and dynamics, root litter as a substrate for decomposers is more heterogeneous than leaf litter (Lõhmus and Ivask 1995). It includes woody roots of several diameter classes. According to Bayer et al. (2013), cellulose substrates (xylan, cellulose and lignin) are decomposed by various strains of polysaccharide-degrading microbes while this process is aided by other fungi and bacteria. The walls of the plant cells consist of a mix of three major components with an average share of 40% cellulose, 30% hemicellulose, and 20% lignin, which varies according to the type and part of the plant (Ibid.).

The effect of tree species on decomposition dynamics was not revealed: roots with the same diameter decomposed at a similar rate for both species. Although nitrogen concentration and the C:N ratio varied significantly among the substrates (Table 3), there was no significant difference in the decomposition rate.

Nitrogen release

The share of the N input from aboveground and belowground litter fluxes may vary by a large extend in different forest ecosystems. In current study, the N flux from aboveground litter in the soil was the main N input from decomposed organic matter for both studied fast growing tree species. It is caused by a significantly larger mass (Table 6) as well as faster decomposition of leaf litter than root litter (Figures 1, 4, and 5). From the point of view concerning the nitrogen budget in both stands the N input from fine roots plays a modest role (Uri et al. 2011; Aosaar et al. 2016). However, actual annual N release from root litter is larger than Table 6 reflects since annual fine root production (FRP) is a steady state process in soil. The production, dying and decomposition of fine roots in closed canopy forests are continuous long lasting processes and FRP ensuring steady state nutrient and carbon flux into the soil (Meyer et al. 2013; Uri et al. 2017a, Uri et al. 2017b; Varik et al. 2015).

Litterbag method

The litterbag method is widely used for decomposition experiments and, like any other method, it has advantages as well as disadvantages. A majority of litter decomposition studies (87%) were conducted with the buried litterbag method (Silver and Miya 2001). It is a basic method for this kind of experiments and is relatively easy to use. However, the main disadvantage is that the environmental conditions affecting decomposition are different from natural conditions (Šlapokas and Granhall 1991a). Several authors have noted that the activity of some soil macrofauna, especially earthworms, isopods, gastropods and millipedes, is more or less excluded resulting in an underestimation in decomposition rate. Mesh size alters microbial and physical processes in the course of decomposition, large mesh size excludes meso- and macrofauna, whereas smaller mesh size impedes the exchange of gas, water, nutrients and microorganisms (Lecerf 2017). The absence of the macrofauna became evident in earlier studies where weight loss was larger in the case of litterbags with larger mesh size than with smaller mesh size (Šlapokas and Granhall 1991a, Silver and Miya 2001). Mesh size affects the macrofauna entering the litter bags. Hopkins et al. (1990) studied the effect of mesh size and found significant difference in decomposition rate between the mesh sizes. In litterbag method it is not possible to separate decomposition losses from leaching and comminution. With larger mesh size also comminution losses out of litterbags can increase.

Some authors (Bloomfield et al. 1993; Dornbush et al. 2002; Fisk et al. 2011; Li et al. 2015) have stated that also the preparation of litter, especially roots, may disrupt the rhizosphere associations developed during their lifetime and decrease the abundance of present microbiota, which in turn results in low decay rates. Also the drying process may have had an effect

on decomposition rate as the dry litter takes time to take up moisture to level off with the environment.

Moreover, there may occur a delay before decomposers invade the bags; also soil structure will be disturbed by inserting meshbags into the soil. Still, this method is mostly suitable for comparing decomposition dynamics for different species or for different sites (soils). By excluding the larger soil fauna, it is still possible to compare the decomposition of different substrates by bacteria and fungi. According to the study by Sun et al. (2013) the remaining mass of roots decomposing in litterbags and intact cores differed between 7% and 21%, being higher in litterbags. Other studies have also confirmed the misrepresentation of the decomposition rate and nutrient release dynamics of plant litter in mesh bags (McClaugherty et al. 1984; Whitford et al. 1988; Van Vuuren et al. 1993; Dornbush et al. 2002; Li et al. 2015). According to results of previously mentioned studies the intact core method is a possible alternative when studying the rate of decomposition of plant litter.

The difference between decomposition rates in free soil and in the litterbag is probably more significant for fertile soils where the effect of earthworms is more apparent, like in our case. The abundance of earthworms is related to soil type and moisture, pH and organic matter content (Edwards and Bohlen 1996). A large biomass of earthworms is often inherent in fertile soils and their contribution to the decomposition processes of organic matter is crucial (Ivask and Truu 1998). At poor sites (e.g. podzols, sandy soils) earthworms are missing or their abundance is very low. It can be assumed that the difference between decomposition rates in the litterbag and in free soil is probably not so significant.

The use of this method did not yield definitive results for estimating the decomposition of various types of organic litter in actual natural conditions. In the present case, the remaining mass of dry grey alder or silver birch leaves after 1 year of decomposition accounted for at least 40% of the initial value. Actually, it was visually seen that already in early summer (i.e. 7 months after litterfall) all leaf litter had disappeared from soil surface in both studied stands. Moreover, according to our results (Figure 1), even as late as three years after the incubation of the samples, roughly 20% of litter was left. If the results of this study reflected the real situation, then the organic forest floor layer in both stands should be formed of decaying leaf litter (remaining organic matter should accumulate every year). The actual leaf litter decomposition process is very fast in natural conditions and released N and C accumulate in the upper soil humus layer (Uri et al. 2011, 2014). Considering that the average annual leaf litter dry mass in silver birch stand varies from 1.7 to 3.4 Mg ha^{-1} (Aosaar et al. 2016) and assuming that during the first year only 40% of leaf litter is decomposed, then the remaining dry mass after one year should be 0.7–1.4 Mg ha^{-1}. Studies (Starr et al. 2004; Erkan et al. 2018) have found a significant relationship between litterfall and some stand properties, among them site type (site fertility), stand age, number of stems, crown closure, basal area, stand stem volume, above-ground biomass, mean annual volume increment, elevation and latitude.

In the current study we found root residues in litterbags even as late as 9 (for silver birch) and 11 years (for grey alder) after incubation and they maintained their recognizable physical form as roots. It is evident that in natural conditions both fine roots ($d < 2$ mm) as well as the roots of the coarser fraction ($2 < d < 5$ mm) decompose into an amorphous mass and disappear in a few years, which was confirmed also by our fine root studies at the same sites. Several studies have been conducted on fine root biomass (FRB) and fine root production (FRP) in one and the same grey alder stand (Uri et al. 2002, 2009, 2011; Aosaar et al. 2013). The FRB was a very stable parameter for this stand at different ages, being 870 and 810 kg ha^{-1} in the 10-year-old stand and 17-year-old stand (Aosaar et al. 2013). At the same time, fine root necromass in the soil was very modest for both sampling periods (190 and 110 kg ha^{-1}, respectively). Taking into account that the annual FRP was 530 kg ha^{-1} (Aosaar et al. 2013) and the total decomposition of fine roots takes more than 10 years, fine root necromass in the soil must be enormous. Actually, fine root necromass was very low, indicating that the real decomposition dynamics of fine roots in natural conditions is much faster than it is in litterbags. Similar results were obtained also in the birch stand where the annual fine root production was estimated at 890 kg ha^{-1} and FRB was estimated at 1350 kg ha^{-1} yr^{-1} (Varik et al. 2015) fine root necromass in young silver birch stands was between 200 and 250 kg ha^{-1} yr^{-1} (Varik et al. 2013), which confirms that conditions for decomposition inside litterbags are significantly different from natural conditions.

Conclusions

We hypothesized that both the leaf litter and root litter of grey alder decomposed more intensively compared to the leaf and root litter of birch because of their higher nitrogen content and a more favourable C:N ratio. The results contradicted this hypothesis; the decomposition dynamics of grey alder and silver birch leaves and roots was not significantly different. For both species, the decomposition of the coarser root fraction ($2 < d < 5$ mm) was faster than the decomposition of the fine roots ($d < 2$ mm). The release of nitrogen from the decomposition of leaves and roots differs multiple times, being higher in the leaves. The litterbag method is suitable for comparing the decomposition dynamics of different organic substrates in similar soil conditions but it does not reflect the actual process that takes place in natural conditions.

Acknowledgements

We thank Mrs. Ester Jaigma for revising the English text of the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This study was supported by the Institutional Research Funding IUT21- 04 of the Estonian Ministry of Education and Research and by the Estonian Science Foundation [grant number 5748] as well as by the project of the Estonian University of Life Sciences [T170053MIMK].

ORCID

Gunnar Morozov http://orcid.org/0000-0002-9442-9929
Jürgen Aosaar http://orcid.org/0000-0002-7711-2014
Mats Varik http://orcid.org/0000-0002-6633-1967
Hardo Becker http://orcid.org/0000-0002-1150-4808

References

Ågren G, Bosatta E. 1996. Theoretical ecosystem ecology: understanding element cycles. Cambridge: Cambridge University press.
Aosaar J, Mander Ü, Varik M, Becker H, Morozov G, Maddison M, Uri V. 2016. Biomass production and nitrogen balance of naturally afforested silver birch (*Betula pendula* Roth.) stand in Estonia. Silva Fenn. 50 (4):1–19.
Aosaar J, Varik M, Lõhmus K, Ostonen I, Becker H, Uri V. 2013. Long-term study of above- and below-ground biomass production in relation to nitrogen and carbon accumulation dynamics in a grey alder (*Alnus incana* (L.) Moench) plantation on former agricultural land. Eur J For Res. 132:737–749.
Aosaar J, Varik M, Uri V. 2012. Biomass production potential of grey alder (Alnus incana (L.) Moench.) in Scandinavia and Eastern Europe: a review. Biomass Bioenerg. 45:11–26.
Asplund J, Hustoft E, Nybakken L, Ohlson M, Lie MH. 2017. Litter impair spruce seedling emergence in beech forests: a litter manipulation experiment. Scand J Forest Res. 33(4):332–337.
Bayer EA, Shoham Y, Lamed R. 2013. Lignocellulose-decomposing bacteria and their enzyme systems. In: Rosenberg E, DeLong EF, Lory S, Stackebrandt E, Thompson F, editors. The prokaryotes. Berlin: Springer; p. 215–266.
Berg B. 1984. Decomposition of root litter and some factors regulating the process: long-term root litter decomposition in a Scots pine forest. Soil Biol Biochem. 16:609–617.
Berg B. 1986. Nutrient release from litter and humus in coniferous forest soils – a mini-review. Scand J Forest Res. 1:350–369.
Berg B. 2000. Litter decomposition and organic matter turnover in northern forest soils. Forest Ecol Manag. 133(1–2):13–22.
Berg B, Staaf H. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. Ecol Bull. 33:163–178.
Berg B, Wessen B, Ekbohm G. 1982. Nitrogen level and lignin decomposition in Scots pine needle litter. Oikos. 38:291–296.
Bloomfield J, Vogt KA, Vogt DJ. 1993. Decay rate and substrate quality of fine roots and foliage of two tropical tree species in the Luquillo experimental forest, Puerto Rico. Plant Soil. 150:233–245.
Bocock KL. 1963. The digestion and assimilation of food by Glomeris marginata. In: Doeksen J, Van der Drift J, editors. Soil organisms. Amsterdam: North Holland Publishing; p. 85–91.
Bonan GB. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science. 320:1444–1449.
Brunner I, Bakker MR, Björk RG, Hirano Y, Lukac M, Aranda X, Børja I, Eldhuset TD, Helmisaari HS, Jourdan C, et al. 2013. Fine-root turnover rates of European forests revisited: an analysis of data from sequential coring and ingrowth cores. Plant Soil. 362(1–2):357–372.
Brunner I, Godbold DL. 2007. Tree roots in a changing world. J For Res. 12 (2):78–82.
Camiré C, Côté B, Brulotte S. 1991. Decomposition of roots of black alder and hybrid poplar in short-rotation plantings: Nitrogen and lignin control. Plant Soil. 138(1):123–132.
Chamier AC. 1987. Effect of pH on microbial degradation of leaf litter in seven streams of the English Lake District. Oecologia. 71:491–500.
Coûteaux MM, Bottner P, Berg B. 1995. Litter decomposition, climate and litter quality. Trends Ecol Evol. 10(2):63–66.
Crawley MJ. 2007. The R book. Hoboken (NJ): John Wiley & Sons Ltd.
Dilly O, Munch JC. 1996. Microbial biomass content, basal respiration and enzyme activities during the course of decomposition of leaf litter in a black alder (*Alnus glutinosa* (L.) Gaertn.) forest. Soil Biol Biochem. 28:1073–1081.
Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J. 1994. Carbon pools and flux of global forest ecosystems. Science. 263:185–190.
Dornbush ME, Isenhart TM, Raich JW. 2002. Quantifying fine-root decomposition: an alternative to buried litterbags. Ecology. 83:2985–2990.
Edwards CA, Bohlen PJ. 1996. Biology and ecology of earthworms. 3rd ed. London: Chapman & Hall.
Erkan N, Comez A, Aydin AC, Denli O, Erkan S. 2018. Litterfall in relation to stand parameters and climatic factors in Pinus brutia forests in Turkey. Scand J Forest Res. 33(4):338–346.
Estonian Weather Service. 2017. Weather observation data for Estonia. [accessed 2017 May 13]. http://www.ilmateenistus.ee/?lang = en/.
Fan P, Guo D. 2010. Slow decomposition of lower order roots: a key mechanism of root carbon and nutrient retention in the soil. Oecologia. 163:509–515.
Fang H, Mo J, Peng S, Li Z, Wang H. 2007. Cumulative effects of nitrogen additions on litter decomposition in three tropical forests in southern China. Plant Soil. 297(1–2):233–242.
Fisk MC, Fahey TJ, Sobieraj JH, Costello AM. 2011. Rhizosphere disturbance influences fungal colonization and community development on dead fine roots. Plant Soil. 341:279–293.
Goebel M, Hobbie SE, Bulaj B, Zadworny M, Archibald DD, Oleksyn J, Reich PB, Eissenstat DM. 2011. Decomposition of the finest root branching orders: linking belowground dynamics to fine-root function and structure. Ecol Monogr. 81:89–102.
Granhall U. 1994. Biological fertilization. Biomass Bioenerg. 6:81–91.
Grüneberg E, Ziche D, Wellbrock N. 2014. Organic carbon stocks and sequestration rates of forest soils in Germany. Glob Change Biol. 20:2644–2662.
Hopkins DW, Ibrahim DM, O'Donnell A, Shiel R. 1990. Decomposition of cellulose, soil organic matter and plant litter in a temperate grassland soil. Plant Soil. 124(1):79–85.
Horodecki P, Jagodziński AM. 2017. Tree species effects on litter decomposition in pure stands on afforested post-mining sites. Forest Ecol Manag. 406:1–11.
Howard PJA, Howard DM. 1974. Microbial decomposition of tree and shrub leaf litter. Oikos. 25:341–352.
Hynynen J, Niemistö P, Viherä-Aarnio A, Brunner A, Hein S, Velling P. 2010. Silviculture of birch (*Betula pendula* Roth. and *Betula pubescens* Ehrh.) in Northern Europe. Forestry. 83(1):103–119.
Hytönen J, Saarsalmi A. 2009. Long-term biomass production and nutrient uptake of birch, alder and willow plantations on cut-away peatland. Biomass Bioenerg. 33:1197–1211.
Ivask M, Truu J. 1998. The relationship of Estonian earthworms to local habitat and soil factors. Pedobiologia. 42:378–384.
Kavvadias VA, Alifragis D, Tsiontsis A, Brosfas G, Stamatelos G. 2001. Litterfall, litter accumulation and litter decomposition rates in four forest ecosystems in northern Greece. Forest Ecol Manag. 144:113–127.
Keyes MR, Grier CC. 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Can J Forest Res. 11:599–605.
Krueger I, Schulz C, Borken W. 2017. Stocks and dynamics of soil organic carbon and coarse woody debris in three managed and unmanaged temperate forests. Eur J For Res. 136:123–137.
Lavelle P, Blanchart E, Martin A, Martin S, Spain A. 1993. A hierarchical model for decomposition in terrestrial ecosystems: application to soils in the humid tropics. Biotropica. 25(2):130–150.
Lecerf A. 2017. Methods for estimating the effect of litterbag mesh size on decomposition. Ecol Model. 362:65–68.
Li A, Fahey TJ, Pawlowska TE, Fisk MC, Burtis J. 2015. Fine root decomposition, nutrient mobilization and fungal communities in a pine forest ecosystem. Soil Biol Biochem. 83:76–83.
Lõhmus K, Ivask M. 1995. Decomposition and nutrient dynamics of fine roots of Norway spruce (*Picea abies* (L.) Karst.) at different sites. Plant Soil. 168/169:89–94.
Lõhmus K, Kuusemets V, Ivask M, Teiter S, Augustin J, Mander Ü. 2002. Budgets of nitrogen fluxes in riparian grey alder forests. Arch Hydrobiol. 141:321–332.

Lõhmus K, Truu M, Truu J, Ostonen I, Kaar E, Vares A, Uri V, Alama S, Kanal A. 2006. Functional diversity of culturable bacterial communities in the rhizosphere in relation to fine-root and soil parameters in alder stands on forest, abandoned agricultural, and oil-shale areas. Plant Soil. 283:1–10.
Lovett GM, Weathers KC, Arthur MA, Schultz JC. 2004. Nitrogen cycling in a northern hardwood forest: Do species matter? Biogeochemistry. 67 (3):289–308.
Maloney DC, Lamberti GA. 1995. Rapid decomposition of summer-input leaves in a northern Michigan stream. Am Midl Nat. 133:184–195.
Mander Ü, Kuusemets V, Ivask M. 1995. Nutrient dynamics of riparian ecotones: a case study from the Porijõgi River catchments. Landscape Urban Plan. 31(1–3):333–348.
McClaugherty CA, Aber JD, Melillo JM. 1984. Decomposition dynamics of fine roots in forested ecosystems. Oikos. 42:378–386.
McClaugherty C, Berg B. 1987. Cellulose, lignin and nitrogen levels as rate regulating factors in late stages of forest litter decomposition. Pedobiologia. 30:101–112.
Meentemeyer V, Berg B. 1986. Regional variation in rate of mass loss of *Pinus sylvestris* needle litter in Swedish pine forests as influenced by climate and litter quality. Scand J Forest Res. 1:167–180.
Meyer A, Tarvainen L, Nousratpour A, Björk RG, Ernfors M, Grelle A, Klemedtsson ÅK, Lindroth A, Räntfors M, Rütting T, et al. 2013. A fertile peatland forest does not constitute a major greenhouse gas sink. Biogeosciences. 10:7739–7758.
Mikola P. 1958. Liberation of nitrogen from alder leaf litter. Acta Forestal Fenn. 67(1):1–10.
Ormerod SJ, Rundle SD, Lloyd EC, Douglas AA. 1993. The influence of riparian management on the habitat structure and macroinvertebrate communities of upland streams draining plantation forests. J Appl Ecol. 30:13–24.
Palviainen M, Finér L. 2015. Decomposition and nutrient release from Norway spruce coarse roots and stumps – a 40-year chronosequence study. Forest Ecol Manag. 358:1–11.
Palviainen M, Finér L, Kurka AM, Mannerkoski H, Piirainen S, Starr M. 2004. Decomposition and nutrient release from logging residues after clear-cutting of mixed boreal forest. Plant Soil. 263(1):53–67.
Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, et al. 2011. A large and persistent carbon sink in the world's forests. Science. 333(6045):988–993.
Peng Y, Thomas SC, Dalung T. 2008. Forest management and soil respiration: implications for carbon sequestration. Environ Rev. 16:93–111.
Persson HA. 1978. Root dynamics in a young scots pine stand in central Sweden. Oikos. 30:508–519.
Persson HA. 1983. The distribution and productivity of fine roots in boreal forests. Plant Soil. 71:87–101.
Persson H. 1979. Fine-root production, mortality and decomposition in forest ecosystems. Vegetatio. 41:101–109.
Persson T, Bååth E, Clarholm M, Lundkvist H, Söderström B, Sohlenius B. 1980. Trophic structure, biomass dynamics and carbon metabolism of soil organisms in a scots pine forest. Ecol Bull. 32:419–459.
Prescott CE. 2010. Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? Biogeochemistry. 101:133–149.
Püttsepp Ü, Lõhmus K, Koppel A. 2007. Decomposition of fine roots and α-cellulose in a short rotation willow (Salix spp.) plantation on abandoned agricultural land. Silva Fenn. 41(2):247–258.
Rytter L. 1990. Biomass and nitrogen dynamics of intensively grown grey alder plantations on peatland [dissertation]. Uppsala: Swedish University of Agricultural Sciences.
Rytter L. 1995. Effects of thinning on the obtainable biomass, stand density, and tree diameters of intensively grown grey alder plantations. Forest Ecol Manage. 73:133–143.
Rytter L. 1996. The potential of grey alder plantation forestry. In: Perttu K, Koppel A, editors. Short rotation willow coppice for renewable energy and improved environment. Uppsala: Swedish University of Agricultural Sciences; p. 89–94.
Rytter RM. 2013. The effect of limited availability of N or water on C allocation to fine roots and annual fine root turnover in *Alnus incana* and *Salix viminalis*. Tree Physiol. 33:924–939.
Rytter L, Rytter RM. 2016. Growth and carbon capture of grey alder (*Alnus incana* (L.) Moench.) under North European conditions – estimates based on reported research. Forest Ecol Manag. 373:56–65.
Saarsalmi A. 1995. Nutrition of deciduous tree species grown in short rotation stands [dissertation]. University of Joensuu.
Scott NA, Binkley D. 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sites. Oecologica. 111 (2):151–159.
Silver WL, Miya RK. 2001. Global patterns in root decomposition: comparisons of climate the litter quality effects. Oecologia. 129:407–419.
Šlapokas T, Granhall U. 1991a. Decomposition of willow-leaf litter in a short-rotation forest in relation to fungal colonization and palatability for earthworms. Biol Fert Soils. 10:241–248.
Šlapokas T, Granhall U. 1991b. Decomposition of litter in fertilized short-rotation forests on a low-humidified peat bog. Forest Ecol Manag. 41 (1-2):143–165.
Starr M, Saarsalmi A, Hokkanen T, Merilä P, Helmisaari HS. 2004. Models of litterfall production for scots pine (*Pinus sylvestris* L.) in Finland using stand, site and climate factors. Forest Ecol Manag. 205 (1–3):215–225.
Sun T, Dong L, Zhang L, Wu Z, Wang Q, Li Y, Zhang H, Wang Z. 2016. Early stage fine-root decomposition and its relationship with root order and soil depth in a Larix Gmelinii plantation. Forests. 7(10):234.
Sun T, Mao Z, Dong L, Hou Y, Wang X. 2013. Further evidence for slow decomposition of very fine roots using two methods: litterbags and intact cores. Plant Soil. 366:633–646.
Swift MJ, Heal OW, Anderson JM. 1979. Decomposition in terrestrial ecosystems. Studies in ecology, Vol. 3. Berkeley/Los Angeles: Blackwell Scientific/University of California Press.
Taylor BR, Parkinson D, Parsons WFJ. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology. 70:97–104.
Tian G, Kang BT, Brussaard L. 1992. Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions – decomposition and nutrient release. Soil Biol Biochem. 24 (10):1051–1060.
Tripathi SK, Singh KP. 1992. Nutrient immobilization and release patterns during plant decomposition in a dry tropical bamboo savanna, India. Biol Fert Soils. 14(3):191–199.
Tripathi SK, Sumida A, Shibata H, Ono K, Uemura S, Kodama Y, Hara T. 2006. Leaf litterfall and decomposition of different above- and below-ground parts of birch (Betula ermanii) trees and dwarf bamboo (Sasa kurilensis) shrubs in a young secondary forest in Northern Japan. Biol Fert Soils. 43:237–246.
Uri V, Aosaar J, Varik M, Becker H, Ligi K, Padari A, Kanal A, Lõhmus K. 2014. The dynamics of biomass production, carbon and nitrogen accumulation in grey alder (*Alnus incana* (L.) Moench) chronosequence stands in Estonia. Forest Ecol Manag. 327:106–117.
Uri V, Kukumägi M, Aosaar J, Varik M, Becker H, Morozov G, Karoles K. 2017a. Ecosystems carbon budgets of differently aged downy birch stands growing on well-drained peatlands. Forest Ecol Manag. 399:82–93.
Uri V, Kukumägi M, Aosaar J, Varik M, Becker H, Soosaar K, Morozov G, Ligi K, Padari A, Ostonen I, Karoles K. 2017b. Carbon budgets in fertile grey alder (*Alnus incana* (L.) Moench.) stands of different ages. Forest Ecol Manag. 396:55–67.
Uri V, Lõhmus K, Kiviste A, Aosaar J. 2009. The dynamics of biomass production in relation to foliar and root traits in a grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural land. Forestry. 82 (1):61–74.
Uri V, Lõhmus K, Kund M, Tullus H. 2008. The effect of land use type on net nitrogen mineralization on abandoned agricultural land: silver birch stand versus grassland. Forest Ecol Manag. 255(1):226–233.
Uri V, Lõhmus K, Mander Ü, Ostonen I, Aosaar J, Maddison M, Helmisaari HS, Augustin J. 2011. Long-term effects on the nitrogen budget of a short-rotation grey alder (*Alnus incana* (L.) Moench) forest on abandoned agricultural land. Ecol Eng. 37(6):920–930.
Uri V, Lõhmus K, Ostonen I, Tullus H, Lastik R, Vildo M. 2007. Biomass production, foliar and root characteristics and nutrient accumulation in

young silver birch (*Betula pendula* Roth.) stand growing on abandoned agricultural land. Eur J For Res. 126(4):495–506.
Uri V, Tullus H, Lohmus K. 2002. Biomass production and nutrient accumulation in short-rotation grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural land. Forest Ecol Manag. 161:169–179.
Van Vuuren MMI, Berendse F, De Visser W. 1993. Species and site differences in the decomposition of litters and roots from wet heathlands. Can J Botany. 71:167–173.
Vares A. 2001. Sanglepa (*Alnus glutinosa* (L.) Gaertn.) lehevarise lagunemine ja lämmastiku dünaamika Eesti kliimatingimustes [Decomposition and nitrogen dynamics in black alder (Alnus glutinosa (L.) Gaertn.) leaf litter in the climatic conditions in Estonia]. Metsanduslikud uurimused. 35:149–155. Estonian.
Varik M, Aosaar J, Ostonen I, Lõhmus K, Uri V. 2013. Carbon and nitrogen accumulation in belowground tree biomass in a chronosequence of silver birch stands. Forest Ecol Manag. 302:62–70.
Varik M, Kukumägi M, Aosaar J, Becker H, Ostonen I, Lõhmus K, Uri V. 2015. Carbon budgets in fertile silver birch (*Betula pendula* Roth) chronosequence stands. Ecol Eng. 77:284–296.
Vogt KA, Grier CC, Gower ST, Sprugel DG, Vogt DJ. 1986. Overestimation of net root production: a real or imaginary problem? Ecology. 67:577–579.
Vogt KA, Grier CC, Meier CE, Keyes MR. 1983. Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in Western Washington, as affected by fine-root input. Ecol Monogr. 53 (2):139–157.
Vogt KA, Vogt DJ, Palmiotto PA, Boon P, O'Hara J, Asbjornsen H. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil. 187:159–219.
Waksman SA. 1952. Soil microbiology. New York: Wiley.
Whitford WG, Stinnett K, Anderson J. 1988. Decomposition of roots in a Chihuahuan desert ecosystem. Oecologia. 75:8–11.
Xiong Y, Fan P, Fu S, Zeng H, Guo D. 2013. Slow decomposition and limited nitrogen release by lower order roots in eight Chinese temperate and subtropical trees. Plant Soil. 363:19–31.
Yearbook Forest. 2016. Compiled by Estonian Environmental Information Centre. Tartu 2017. In Estonian. [accessed 2017 Nov 4]. http://www.keskkonnaagentuur.ee/sites/default/files/mets2016_08.08.pdf.
Zhou Z, Shangguan Z. 2007. Vertical distribution of fine roots in relation to soil factors in *Pinus tabulaeformis* Carr. forest of the Loess Plateau of China. Plant Soil. 291:119–129.

Appendices

Appendix 1. Precipitation and annual length of vegetation period in Võru weather station throughout the years 1996–2013 (Estonian Weather Service).

Year of measuring	Length of vegetation period (days)	Precipitation (mm)	Precipitation in vegetation period (mm)	Average air temperature in vegetation period (°C)
1996	204	539.3	137.3	12.7
1997	169	779.8	214.5	13.6
1998	196	831.5	206.1	13.5
1999	203	609.8	167.2	14.5
2000	214	590.0	158.1	12.8
2001	203	666.6	158.0	14.0
2002	177	462.7	117.0	15.1
2003	186	797.6	214.3	13.5
2004	206	727.5	182.2	13.3
2005	183	556.4	172.2	13.5
2006	203	537.9	150.0	13.9
2007	191	655.5	143.3	14.4
2008	217	794.4	228.8	12.3
2009	170	771.9	172.4	13.1
2010	195	897.7	239.5	14.3
2011	203	575.8	166.7	14.2
2012	194	800.8	170.3	13.6
2013	209	532.1	148.3	14.3

Appendix 2. Parameter estimates of ANOVA function (2) for estimation of the decomposition dynamics of grey alder and silver birch leaf and root litter (parameter ln (c) = 0 for Silver birch on the third and fourth rows and for the roots 2–5 mm on the first and second rows).

			ln(c)			
Substrate	ln(a)	b	for the	value	p-value	R^2
Grey alder roots	−2.5652	−0.3244	<2 mm	−0.2409	0.045	0.836
Silver birch roots	−2.0892	−0.4637	<2 mm	−0.1571	0.093	0.925
Roots <2 mm	−2.7570	−0.3169	Grey alder	−0.0730	0.540	0.794
Roots 2-5 mm	−2.2822	−0.4082	Grey alder	−0.0161	0.876	0.895

II

Becker, H.; Aosaar, J., Varik, M., **Morozov, G.**, Aun, K., Mander, Ü., Soosaar, K., Uri, V. (2018). Annual net nitrogen mineralization and litter flux in well-drained downy birch, Norway spruce and Scots pine forest ecosystems. Silva Fennica, 52 (4), 1−18. 10.14214/sf.10013.

Silva Fennica vol. 52 no. 4 article id 10013
Category: research article
https://doi.org/10.14214/sf.10013
SILVA FENNICA
http://www.silvafennica.fi

ISSN-L 0037-5330 | ISSN 2242-4075 (Online)
The Finnish Society of Forest Science

Hardo Becker[1], Jürgen Aosaar[1], Mats Varik[1], Gunnar Morozov[1], Kristiina Aun[1], Ülo Mander[2], Kaido Soosaar[2] and Veiko Uri[1]

Annual net nitrogen mineralization and litter flux in well-drained downy birch, Norway spruce and Scots pine forest ecosystems

Becker H., Aosaar J., Varik M., Morozov G., Aun K., Mander Ü., Soosaar K., Uri V. (2018). Annual net nitrogen mineralization and litter flux in well-drained downy birch, Norway spruce and Scots pine forest ecosystems. Silva Fennica vol. 52 no. 4 article id 10013. 18 p. https://doi.org/10.14214/sf.10013

Highlights

- The net nitrogen mineralization (NNM) flux in drained peat soils depends largely on the C/N ratio and tree species.
- The soil NNM process is affected by trees through organic litter input into soil.
- Pine stand in low-fertility drained transitional bog is dominated by net ammonification.
- Birch and spruce stands on the fertile drained peat soil with higher pH and N content are dominated by net nitrification.

Abstract

The main aim of the current study was to estimate the annual net nitrogen mineralization (NNM) flux in stands of different tree species growing on drained peatlands, as well as to clarify the effect of tree species, soil properties and litter on annual NNM dynamics. Three study sites were set up in May 2014: a downy birch (*Betula pubescens* Ehrh.) stand and a Norway spruce (*Picea abies* (L.) Karst.) stand in *Oxalis* full-drained swamp (ODS) and a Scots pine (*Pinus sylvestris* L.) stand in *Myrtillus* full-drained swamp (MDS). The NNM flux was estimated using the *in situ* method with incubated polyethylene bags. The highest value of NNM was found in stands that were growing on fertile ODS: 127.5 kg N ha^{-1} yr^{-1} and 87.7 kg N ha^{-1} yr^{-1}, in the downy birch stand and in the Norway spruce stand, respectively. A significantly lower annual NNM flux (11.8 kg N ha^{-1} yr^{-1}) occurred in the Scots pine stand growing in MDS. Nitrification was highest at fertile ODS sites and ammonification was the highest at the low fertility MDS site. For all study sites, positive correlation was found between soil temperature and NNM intensity. The difference in annual NNM between the downy birch stand and the Norway spruce stand growing on similar drained fertile peatlands was due to litter quality. The annual N input into the soil through leaf litter was the highest at the downy birch site where also the C/N ratio of litter was the lowest. The second highest N input into the soil was found in the spruce stand and the lowest in the pine stand.

Keywords *Betula pubescens*; *Picea abies*, *Pinus sylvestris*, ammonification; drained peatland forests; effect of tree species; swamp; nitrification; transitional bog
Addresses [1]Chair of Silviculture and Forest Ecology, Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Friedrich Reinhold Kreutzwaldi 1, 51014 Tartu, Estonia; [2]Department of Geography, Institute of Ecology & Earth Sciences, University of Tartu, Ülikooli 18, 50090 Tartu, Estonia
E-mail hardo.becker@emu.ee
Received 12 June 2017 **Revised** 14 September 2018 **Accepted** 17 September 2018

1 Introduction

Forest drainage is an important and widely used forest management practice for increasing site fertility and forest growth in excessively moist soils and peatlands in the boreal and hemiboreal zones. About 15 million ha of peat soils have been drained in the temperate and boreal regions for the purpose to improve forest site fertility (Paavilainen and Päivinen 1995). In Finland, over 5.5 million ha are under drained forests, of which 4.5 million ha grow on peatlands (Peltomaa 2007). In Estonia, the most intensive forest draining was carried out during 1970–1980 and the total area of drained forest formed over 500 000 ha (Yearbook of Forest 2016). Approximately 20% of Estonian forests grow on peatlands, from which 14% are drained (Yearbook of Forest 2016). These forests are diverse; a large share of them are managed regularly and some belong to protected forest areas. After drainage of peatlands, soil organic matter starts to decompose, which can also lead to the increased rate of greenhouse gas (GHG) emission. Several studies have reported intensive soil respiration in drained forests (Martikainen et al. 1993; Silvola et al. 1994; Ojanen et al. 2013). In the light of increased CO_2 emissions and expected global warming, a number of studies have focused on carbon (C) emissions in drained forest (Silvola et al. 1994; Ojanen et al. 2013; Meyer et al. 2013; Birdsey and Pan 2015). However, since nitrogen (N) is strongly related to the C cycle, studies of the N cycle and N mineralization in drained forest ecosystems should be emphasized as well. Nitrogen is one of the mineral elements limiting forest growth in the boreal region (Luo et al. 2004). Thus N availability is an essential factor affecting also C accumulation by plants also, there is strong relationship between forest C and N cycling (Millard et al. 2007). Net nitrogen mineralization (NNM) is an essential flux in whole N cycle of boreal and temperate forests (Zak et al. 1990; Goodale and Aber 2001; Lovett et al. 2002; Uri et al. 2008), since most of the N utilized for plant production is produced by *in situ* mineralization of organic matter (Tate 1995).

The intensity of NNM depends on many factors: soil type, tree species, land use history etc. (Zak et al. 1990; Goodale and Aber 2001; Lovett et al. 2002; Uri et al. 2008). Also soil water content can influence the intensity of NNM (Raison et al. 1987; Stenger et al. 1995; Persson and Wiren 1995). Reduction in soil water content and improvement in soil aeration in drained peatlands also make conditions more favourable for NNM, which improves tree growth and influences ecosystem structure (Silins and Rothwell 1999). Wang et al. (2018) conclude that long term drainage increases nutrient availability and the vegetation changes in response to drainage. Some studies report that the N pool of drained forest can even be higher than the N pool of upland sites (Westman and Laiho 2003). Also a change in the leaching of N in the form of ammonium may be increased after drainage (Laine et al. 1995). When NNM studies mostly focus on mineral soils in different forest ecosystems (Connell et al. 1995; Goodale and Aber 2001; Andersson et al. 2002; Lõhmus et al. 2002; Pajuste and Frey 2003; Uri et al. 2008, 2011; Becker et al. 2015, 2016), then relevant studies focusing on organic soils are still scarce.

This study involved three main tree species that form most part of the stands growing in drained forest ecosystems in Estonia: Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) Karst.) and downy birch (*Betula pubescens* Ehrh.). The main aim of the study was to estimate the annual NNM flux in different stands growing on drained peatlands and to clarify the effect of tree species, soil type and litter quality on annual NNM dynamics. We hypothesized that annual NNM is higher in deciduous (birch) stand than in coniferous (spruce) stand growing on similar organic soils.

2 Materials and methods

2.1 Study sites

Three study sites were set up in May 2014 in the Järvselja experimental forest district (58°16´N, 27°18´E) which is located in the eastern part of Estonia. The area belongs to the hemiboreal vegetation zone (Ahti et al. 1968), which is a transition zone from the temperate to the boreal climate. The Järvselja forest district has a long drainage history (the first drainage systems were set up at the end of the 19th century) and drained forests are widespread in this area. All study sites of different tree species are located on long-term drained forested peatlands (Table 1) and the average distance between the study sites was roughly 5 km. In Estonia, *Oxalis* full-drained swamp (ODS) and *Myrtillus* full-drained swamp (MDS) are the two main forest site types in peatland forest (Yearbook forest 2016). The ODS site type made up 14% and the MDS site type made up 6% of the Järvselja forest district (Korjus et al. 2015). All studied sites had been drained approximately 40–50 years earlier using open ditches. As a result of drainage, groundwater level was normally below 40 cm from surface during the growing season.

At all study sites, a sample plot (20×25 m) was established and the main stand characteristics were measured (Table 1). The main tree species according to the study sites were downy birch, Norway spruce and Scots pine and all stands were naturally regenerated. However, in the spruce stand and in the pine stand, some birch trees were growing as secondary species whose basal area (BA) formed roughly 15% and 10% of total stand BA, respectively.

The soil of the study sites was classified according to World Reference Base for Soil Resources (FAO 2006) (Table 2). The region's long term average precipitation is 650 mm, average temperature is 17 °C in July and –6.7 °C in January and the growing season usually lasts 175–180 days (Kupper et al. 2011). Soil pits were dug at all sites to estimate the soil type as well as its bulk density. The soils and the site types of the birch and spruce stands were similar and the site type was classified as ODS. The pine stand was growing on MDS.

2.2 Incubation method

The NNM experiment was performed by using the method with incubated polyethylene bags (Eno 1960; Uri et al. 2008; Becker et al. 2015, 2016). Polyethylene bags ensure permeability to gases (O_2, CO_2, N_2, etc.), but prevent leaching and the input of soluble N, as well as the direct nitrogen uptake by plants. The dynamics of NNM was studied in the 0–10 cm soil layer at all three study sites from May 2014 to June 2015. At all sites, sampling and incubation were performed at an approximately monthly interval, which has been reported to be an optimal period for changes in

Table 1. Main stand characteristics of the study sites. H – average stand height, $D_{1.3}$ – average breast height diameter, BA – basal area.

Study site	Age (yr)	Stand area (ha)	N (trees ha^{-1})	H (m)	$D_{1,3}$ (cm)	BA (m^2 ha^{-1})	Volume (m^3 ha^{-1})
Downy birch	30	5.1	1660	15	14	24.5	193
Norway spruce	55	0.9	942	17	18,4	25	208
Scotch pine	65	1.3	620	23	22	20.1	218

Table 2. Soil characteristics of the studied stands. C – organic carbon (%), N – Kjeldahl nitrogen (%), P – available (AL) phosphorus (mg kg^{-1}), K 620 available (AL) potassium (mg kg^{-1}), average concentrations are presented for the upper 10 cm soil layer (n = 5), World Reference Base for soil resources (WRB).

Study site	Soil type (WRB 2006)	Peat layer depth (cm)	Soil bulk density (0–10 cm)	pH KCl	N %	C %	P mg/kg	K mg/kg	N storage (t ha^{-1})		C/N (0–10 cm)
									0–10 cm	0–40 cm	
Downy birch	*Drainic Eutric Histosol*	>100	0.20	4.8±0.01	2.6±0.03	39.4±1.01	44.8±1.93	159.0±2.94	5.1	19.9	15.3
Norway spruce	*Drainic Eutric Histosol*	=45	0.18	4.4±0.01	2.7±0.04	33.5±0.9	49.0±7.18	186.9±17.34	4.9	21.5	12.3
Scotch pine	*Drainic Mesic Histosol*	=45	0.14	2.6±0.05	1.4±0.04	39.8±1.3	147.9±15.9	370.4±44.76	1.9	10.6	29.0

the concentration of the mineral forms of N (Adams et al. 1989), and has also been applied in our earlier studies (Uri et al. 2003, 2008, 2011; Becker et al. 2015, 2016). At each sampling session, 24 samples for incubation were taken from all study sites by using a cylindrical soil corer (Ø 48 mm). The internal diameter of the inner part of the corer was 1.6 mm larger than the diameter of the cutting edge to avoid compression of the soil. The intact soil cores were packed in polyethylene bags with a thickness of 18 µm and incubated inside the same hole. Simultaneously with the incubation of a new sample, an adjacent initial sample was taken next to the incubated sample each time. Both the incubated and the initial samples from each sampling place were collected separately and gathered then by three in order to form eight composite samples from the incubated and initial samples, which were transported to the laboratory on the same day. Sampling was done monthly throughout the year, except when the soil was frozen. A more detailed description of the incubation methods has been published earlier in Uri et al. (2003, 2008) and Becker et al. (2015, 2016).

2.3 Litter collection

Aboveground litter was collected in 2015 using seven litter traps installed at each of the three study sites. In the downy birch stand the collecting area of a litter trap was 0.36 m^2 and in the coniferous stands it was 0.53 m^2. Litter was collected from the litter traps at an approximately monthly interval. However, in the autumn when litter fall in the birch stand was more intensive the interval was about two weeks. All collected litter was taken to the laboratory and dried to constant weight. After drying, litter was fractioned according to the tree species growing at the site and all fractions were weighed. As the decomposition of leaf and needle litter is faster compared to branch litter and affects net nitrogen mineralization the most, we considered only the leaf and needle fractions of litter.

2.4 Soil chemical analysis

The Tecator ASN 3313 was employed for testing the soil samples for nitrogen after Kjeldahl. Soil NO_2^--N, NO_3^--N and NH_4^+-N were determined by flow injection analysis with the Tecator ASN 65-32/84 and the Tecator ASN 65-31/84. Soil pH was determined in a 2.5:1 KCl soil (vol/wt) suspension. Available P and K were extracted with ammonium lactate (0.1 M $NH_4CH_3CH(OH)COO^-$ + 0.4M CH_3COOH, pH 3.75). Available phosphorus in the extraction solution was determined by flow injection analysis with of the Tecator ASTN 9/84 and the content of available potassium was determined from the same solution by the flame photometric method. For determination of C_{org} content in the oven-dried samples, the combustion method (1150 °C) was applied using a vario-MAX CNS elemental analyser (ELEMENTAR, Germany).

The samples of litter were analysed for total Kjeldahl nitrogen (N). The block digestion and steam distillation methods were used for testing the plant material (leaves and needles) for N concentration (Tecator AN 300).

2.5 Statistical analysis of the data

Normality of variables was checked using the Lilliefors and Shapiro-Wilk's tests. For multiple comparisons of means, in case the assumptions were satisfied, the t-test was employed to compare the two group means. The correlation matrix was used to estimate relationships. In all cases the level of significance 0.05 was accepted. STATISTICA 7 (StatSoft, Inc., 2013) software was used in all cases.

3 Results

3.1 The soil nitrogen pool and the seasonal dynamics of soil mineral nitrogen

The total N pool for the upper 10 cm soil layer was higher in the birch and spruce stands growing on *Drainic Eutric Histosols* and it was estimated roughly at 5 t N ha^{-1}. In the pine stand on *Drainic Mesic Histosol*, the total N pool for the upper 10 cm soil layer was almost 2 t ha^{-1} (Table 2). The average concentrations of mineral N for the different months were higher in the birch and spruce stands and were significantly lower in the well-drained *Myrtillus*-type pine stand (Fig. 1). There was no significant difference in annual (whole-year dataset) mineral N concentrations in the soil between the spruce and birch stands (t-test, $p > 0.05$). However, when comparing soil N concentrations in the different months for the birch and spruce stands, then they were significantly higher for the spruce stand in May 2014, November 2014 and May 2015 (t-test, $p < 0.05$) (Fig. 1).

The annual dynamics of soil mineral N concentrations was significantly different for the studied *Oxalis* and *Myrtillus* fully drained forest sites (Fig. 1). Both in the birch and spruce stands, soil mineral N concentration peaked in August and November, amounting almost to 70 mg kg^{-1} (Fig. 1). In the pine stand, the mineral N concentration varied between 0.1–2.8 mg kg^{-1} throughout the year and peaked in April when it was only up to 3 mg kg^{-1} (Fig. 2c). In the birch and spruce stands the highest share of soil mineral N was formed of NO_3-N, while in the pine stand NH_4-N was the dominating form of mineral N in the upper soil layer (Fig. 2). Also soil pH was significantly lower in the pine stand (Table 2). The pH of the incubated samples in the birch stand varied between 4.7 and 4.8, in the spruce stand between 4.3 and 4.5 and in the pine stand 2.5 and 2.8. There was no difference between the pH values of the initial and the incubated samples at all studied sites (t-test, $p > 0.05$). Although NH_4-N was almost missing in the soil of the birch stand, it made up 30% of total mineral N in the spruce stand in the different months (Fig. 2).

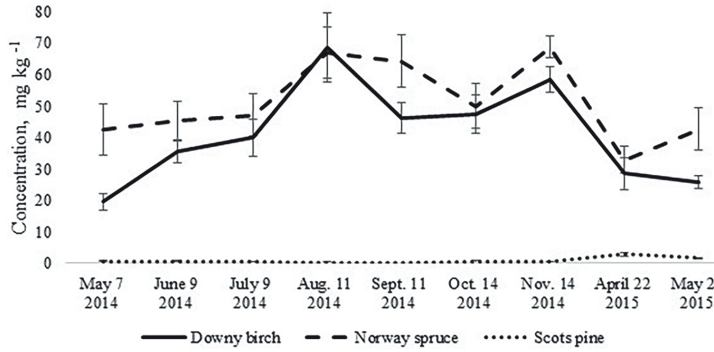


Fig. 1. Mean concentrations of soil mineral nitrogen in the upper 10 cm soil layer of birch, spruce and pine stand. Bars indicate the values of standard error, n = 8 (24 replicates pooled by three).

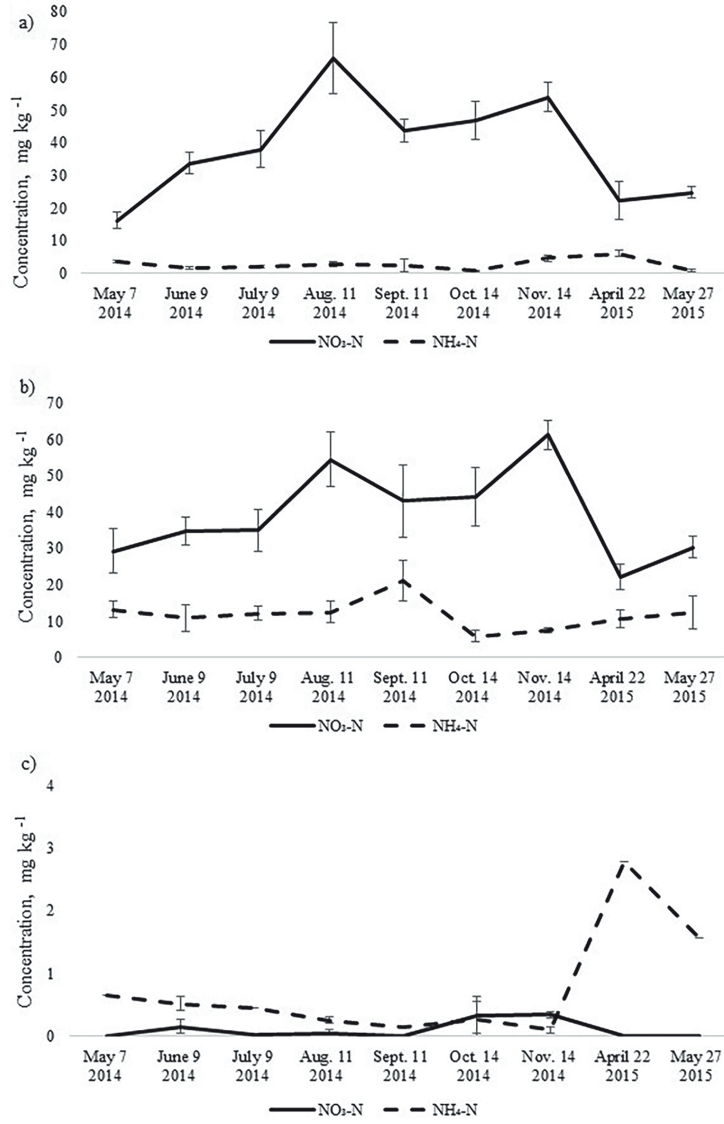


Fig. 2. Mean concentrations of soil NO_3-N and NH_4-N in the upper 10 cm soil layer of a) birch, b) spruce and c) pine stand. Bars indicate the values of standard error, n = 8 (24 replicates pooled by three).

3.2 Annual net nitrogen mineralization

3.2.1 Birch and spruce stands

The intensity of annual NNM was the highest in the birch stand and the lowest in the pine stand (Fig. 3). In the birch stand a peak of NNM occurred in July 2014 (t-test, $p < 0.05$), when NNM intensity exceeded 120 mg N kg day^{-1}, and another peak (109 mg N kg day^{-1}) occurred in June 2015 (t-test, $p < 0.05$). The rate of net nitrification was very high in the birch stand whereas the rate of ammonification was even negative during seven months. There was positive correlation between NNM intensity and soil temperature for the birch stand ($r = 0.78$, $p = 0.013$). However, when we considered the net nitrification and the net ammonification processes separately, positive correlation occurred only between soil temperature and net nitrification ($r = 0.80$, $p = 0.009$). There was no correlation between soil pH and NNM intensity between soil moisture content and NNM intensity for the birch stand.

In the spruce stand, likewise, net nitrification was the dominating process and net ammonification was negative during four months in the study period (Fig. 3). The NNM intensity peaked one month later than in the birch stand (in August), being as high as 100 mg N kg day^{-1} and another peak (61 mg N kg day^{-1}) occurred in May (t-test, $p < 0.05$). There was also strong correlation between NNM intensity and soil temperature ($r = 0.79$, $p = 0.012$) as well as between NO_3-N and soil temperature ($r = 0.79$, $p = 0.011$). The share of net ammonification in total NNM was larger compared with the birch stand, but like for the birch stand, there was no correlation between net ammonification and soil temperature or between pH and NNM intensity.

Annual cumulative NNM was significantly higher in the birch stand compared with the spruce stand (t-test, $p = 0.045$) (Table 3), being almost 130 kg ha^{-1}, which made up 2.4% of the soil N pool of the upper 0–10 cm. In the spruce stand the annual NNM flux was 88 kg ha^{-1}, which accounted for about 1.7% of the upper 0–10 cm soil N pool. At the same time, in both stands the share of net nitrification made up 95%. The share of net ammonification in total NNM in May and October was substantial in the spruce stand (Fig. 3). Yet because of the microbial immobilization of ammonium nitrogen in the other months, total annual net ammonification was still low.

3.2.2 Pine stand

The intensity of NNM in the pine stand had a different pattern form that of the birch and spruce stands which were growing on a more fertile drained peat soil. Overall, it was much lower with peaks in June in both 2014 and 2015. Only in June 2015 was it significantly higher than in the other months (t-test, $p < 0.05$) (Fig. 3). Net ammonification was the highest in the pine stand where nitrification was practically missing. Positive correlation between soil temperature and NNM intensity was found also for the pine stand ($r = 0.74$, $p = 0.023$), but there was no correlation between soil pH and NNM intensity. In all cases, NNM intensity was the lowest in the autumn months (October and November) and cumulative annual NNM was only 12 kg ha^{-1} (Table 3).

3.3 Nitrogen input into soil through litter fall

The annual litter flux in 2015 was around 4 t ha^{-1} at all study sites (Table 4). To calculate the N input into the soil through litter, only leaf litter and needle litter were taken into account as the corresponding fractions have the highest decomposing rate and form the main share of the annual litter flux. In the birch stand, leaf litter was 3.1 t ha^{-1} and contributed the most to the N input (36 kg N ha^{-1}) into the soil among the study sites. In the spruce stand, the needles and the birch

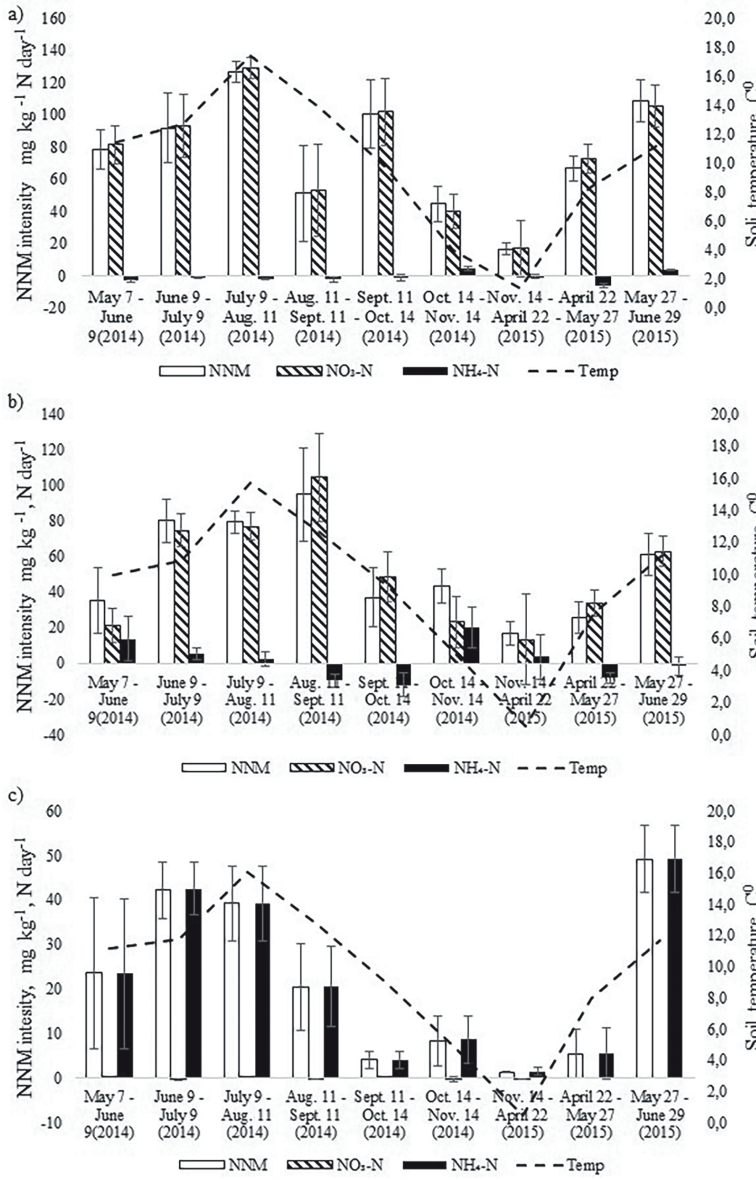


Fig. 3. Dynamics of monthly average soil temperature in the upper 10 cm soil layer and the dynamics of net nitrogen mineralization (NNM) intensity (mg kg^{-1} N day^{-1}) in the a) birch, b) spruce and c) pine stand in 2014–2015. Bars indicate the values of standard error.

Table 3. Annual net nitrification (NO_3-N), annual net ammonification (NH_4-N), total net nitrogen mineralization (NNM) (kg ha^{-1}) and the share of net nitrification (%) in the studied stands.

Study site	NO_3-N ha	NH_4-N ha	NNM	Nitrification
Downy birch	129.3	–1.7	127.5	100.0
Norway spruce	83.3	4.4	87.7	94.9
Scots pine	–0.1	11.8	11.8	0.0

leaves produced 2.8 t ha^{-1} and their total N input into the soil through litter was 25 kg N ha^{-1} (Table 4). In the pine stand, the N input into the soil through litter was the smallest (10 kg N ha^{-1}) and N concentrations in the leaves and needles were also the lowest.

4 Discussion

4.1 Soil nitrogen pool and its dynamics

4.1.1 Birch and spruce

A large soil nitrogen (N) pool is typical of drained eutrophic swamp forests (Westman and Laiho 2003). In this study the total soil N pool in the 0–10 cm upper soil layer in the birch and spruce stands was about 5 t N ha^{-1} and in the soil layer up to 40 cm it even amounted to 20 t N ha^{-1} (Table 2). This exceeds to considerably the N storages reported for mineral soils of the boreal and hemiboreal forest ecosystems (Gundersen 1995; Uri et al. 2003, 2008; Becker et al. 2015, 2016). The large total soil N storage, inherent in organic soils, can be explained by presence of a thick peat layer and high N concentration of peat. However, a large soil N pool does not reflect the amount of N that is actually available for uptake by plants. According to Helmisaari (1995), typically only about 0.1–1% of the soil N pool is available for plants in the form of inorganic N in boreal forests. The corresponding share of 1–3.5% in the upper soil N pool has been found to be available as mineral N (Baldock and Nelson 2000; Uri et al. 2008; Becker et al. 2015). In this study the share of mineral N of the total N pool in the upper 0–10 cm soil layer was in a similar range and varied from 1.7% to 2.4% in the spruce and birch stands, respectively.

The annual dynamics of soil mineral N in the birch and spruce stands demonstrated a similar pattern. There was no difference between these stands in mineral N concentration in the upper 0–10 cm soil layer over the whole-year dataset (t-test, $p > 0.05$). In both stands, soil mineral N

Table 4. Litter characteristics of the studied stands (n = 7).

Stand	Leaves (t ha^{-1})	Needles (t ha^{-1})	Branches (t ha^{-1})	Other (t ha^{-1})	Total	N concentration (%)		N input (kg ha^{-1})	C/N	
						Leaves	Needles		Leaves	Needles
Birch	3.1		0.4	0.1	3.7±0.18	1.14		35.7	42	
Spruce	0.8	2.0	0.9	0.6	4.3±0.16	1.11	0.80	24.9		59
Pine	0.3	2.1	0.5	0.9	3.8±0.15	0.96	0.34	10.0		157

concentration peaked in August and November 2014. The increase of soil mineral N in autumn is a typical pattern which can be explained mainly by the ceased N uptake by plants and by the input of fresh organic matter through litter (Uri et al. 2003, 2008; Becker et al. 2015). Mineral N concentration in the soil was low in spring and increased up to autumn, which is in good accordance with the dynamics of NNM intensity. High soil mineral N concentration during the vegetation period (Fig. 1) is the result of favourable conditions that promote NNM.

4.1.2 Pine stand

As the pine stand was growing on a relatively poor drained oligotrophic peat soil, the content and dynamics of mineral N was different from those of the birch and spruce stands. The total soil N pool in the pine stand was significantly smaller, amounting to 1.9 t N ha^{-1} in the upper 10 cm soil layer. Also the content of soil mineral N was several times lower, which is mainly related to soil properties and site history. It is well known that the concentration of soil mineral N depends on the intensity of NNM and, on the other hand, on plants uptake. The low share of mineral N of the upper soil layer (0.6% of the total soil N pool) in the pine stand could be explained by low NNM intensity. Ammonium N was the prevailing form of mineral N in the pine stand, whereas nitrate N concentration was negligible in all months. The concentration of soil ammonium N varied between 0.45 and 2.8 mg kg^{-1} during the whole study period. This estimate can be considered low since it is roughly ten times as low as the corresponding estimate for a *Rhodococcum* pine stand in Estonia (Kurvits et al. 2004).

4.2 Annual NNM and litter N input

4.2.1 Birch and spruce stands

In this study N mineralization occurred in the upper 0–10 cm soil layer, which is the most active soil part. The upper soil layer is characterized by higher nutrient content, higher microbial biomass and activity as well as the largest fine root biomass (Lõhmus et al. 2006; Uri et al. 2009; Aosaar et al. 2013; Varik et al. 2013). Moreover, according to several studies, most of NNM occurs in the topsoil layer. Connell et al. (1995) concluded that 75–85% of NNM generally takes place in the upper 0–20 cm soil layer. Persson and Wirén (1995) have reported that on average 78% of NNM occurs in the 0–10 cm topsoil layer and the remaining 22%, in the 10–50 cm layer of the mineral soil.

The buried bag method used *in situ* is one of the most common methods for *in situ* NNM studies (Hanselman et al. 2004; Duran et al. 2012) and reflects the actual rate of N mineralization in the soil. Also the method with the covered cylinders may give similar results assuming that the diameter of the incubated soil core is sufficiently large (5 cm) (Hanselman et al. 2004; Duran et al. 2012).

NNM is mainly affected by soil temperature and pH (Tietema and Verstraten 1992) while the effect of soil moisture is not very clear (Uri et al. 2008; Becker et al. 2015, 2016). The effect of soil temperature on NNM intensity was revealed also in the present study, but the effects of pH and soil moisture on NNM were not detected. Although it has been reported that the concentration of soil nitrate N is largely affected by temperature and drainage while the concentration of soil ammonium N depends on soil moisture and precipitation rate (Glina et al. 2016), we did not find any positive correlation between NH_4-N and soil moisture. At the same time, the nitrification process was more favoured in the birch stand than in the spruce stand despite the fact that both were growing on peat soils with similar properties and N content (Table 2). Nitrification was also the major process of N transformation in the spruce stand while ammonification accounted for

roughly 5% of total NNM. In the birch stand, the rate of nitrification was 100% (Table 3). Lower nitrification in the spruce stand can partly be explained by lower soil pH (Table 1), which is evidently the result of more acid needle litter. The favourable range for nitrification is from pH 3.9 to 6.3 (Van Praag and Weissen 1973); low pH often restricts nitrification and almost no nitrification can be detected at pH < 4 (Persson and Wiren 1995). As in both stands the pH values were higher than 4, nitrification was a favoured process in both of them.

Also the annual cumulative NNM flux was different in the birch and spruce stands growing on fertile drained *Drainic Eutric Histosols*, which are nutrient rich and whose pH is relatively high. Annual NNM in the birch and spruce stands was estimated roughly at 130 kg N ha^{-1} yr^{-1} and 90 kg N ha^{-1} yr^{-1}, respectively. This difference is likely due to the difference in the species composition of these stands. Several studies indicate that also the quantity and quality of soil organic matter have a significant effect on NNM intensity, the C/N ratio being one of the key factors (McClaugherty et al. 1985; Zak et al. 1990; Tietema et al.1993). According to literature data (Aber et al. 1989; Scott and Binkley 1997; Magill et al. 2000; Uri et al. 2011; Becker et al. 2015), the annual NNM in deciduous stands varies between 24 kg ha^{-1} yr^{-1} and 200 kg ha^{-1} yr^{-1} and can usually cover a major part of the annual N demand of these stands. An earlier study on mineral soil in Estonia found the annual N mineralization flux to be only 24 kg N ha^{-1} yr^{-1} in a spruce stand (Pajuste and Frey 2003). At a site with low fertility the C/N ratio for a spruce stand growing on *Haplic Podzol* was between 28–31 kg N ha^{-1} yr^{-1} (Pajuste and Frey 2003), which is much higher than the corresponding ratio in our the present study. In a spruce stand, after a clear cut for the purpose of stump harvesting, the annual NNM flux was as high as 200 kg N ha^{-1} yr^{-1} (Becker et al. 2016). In the present study the soil C/N ratio for the upper 0–10 cm layer in the birch and spruce stands was 15.3 and 12.3, respectively (Table 2). These figures are of the same magnitude as those found for fertile forest site types on mineral soils (Cools et al. 2014; Uri et al. 2014, 2015; Varik et al. 2015; Becker et al. 2015, 2016). In Estonian birch stands, aged 13 to 45 years and growing on fertile mineral soils, the soil C/N ratio for the A-horizon has been evaluated to range between 13.6 and 15.8 (Varik et al. 2015).

Soil nitrogen dynamics is strongly related to the carbon cycle (C). Both the downy birch stand (Uri et al. 2017) and spruce stand (unpublished data) were highly productive and acted as C sinks. In forests growing on drained organic soils, the high C uptake by trees can often compensate for intensive soil respiration (Minkkinen et al. 2002; Hargreaves et al. 2003) and in terms of productivity and more effective C sequestration, available soil N is crucial. Stand productivity depended on the co-effect of multiple factors; high annual NNM intensity is one factor which ensures vigorous growth of trees and hence high C accumulation. As a result of the long term drainage of swamps, there has emerged a specific fertile site type which is very favourable for forest management. However, in order to increase the C sequestration ability of stands, also tree species play an important role. Further, reforestation of these areas after clear-cut by more productive tree species like black alder (*Alnus glutinosa* (L.) Gaertn) or Norway spruce (*P. abies*) would be a reasonable option. Still, it should be noted that, despite their high productivity, spruce stands on organic soils may be sensitive to wind throw.

Annual NNM in forest soils has often two peaks, one at the beginning and the other one at the end of the growing season (Nadelhoffer et al. 1984; Uri et al. 2003). In the current study NNM mineralization in both stands peaked at the early in the vegetation period in both years (2014 and 2015). The second peak in the rate of NNM mineralization at the end of the vegetation period occurred in the birch stand but not in the spruce stand.

The negative net ammonification fluxes noted for the spruce stand in the four months of the study period (Fig. 3) can most probably be explained by N immobilization or by gaseous losses of denitrification (Maag and Vinther 1996). Negative available ammonium was oxidized into nitrate.

One characteristic that describes the influence of tree species on NNM is the difference in their litter quality. The difference in the annual NNM flux between the birch stand and the spruce stand was about 30% and the difference in the annual N fluxes that reached the soil through leaf litter and needle litter has the same range (Table 4). Our result about the annual N input into the soil through needle litter is in good accordance with earlier studies (Pajuste and Frey 2003) where the N input into the soil through spruce needles was estimated at 24.2 kg N ha^{-1} yr^{-1}. The impact of tree species on N cycling in forest ecosystems resulted from different soil properties (Lovett et al. 2004). The decomposition rate of litter is strongly affected by leaf nitrogen content (Cotrufo et al. 1995). In this study N content was the highest in the birch leaves and the C/N ratio, which is an essential factor in terms of litter decomposition, was about one third smaller for the birch leaves compared with the spruce needles.

4.2.2 Pine stand

In the studied pine stand, annual NNM was significantly lower than in the birch or spruce stand, being about 12 kg N ha^{-1} yr^{-1}. This can be explained by lower site fertility, on the one hand, and by the quality of organic litter, on the other. The pine stand is growing in the MDS site type with *Drainic Mesic Histosols*, which are known as relatively nutrient poor soils but suitable for pine. In the present case the fertility of the soil is strongly affected by site history; MDS is the result of long term drainage of transitional (mesotrophic) bog. The fertility of such sites is mainly influenced by the previous drainage situation, but first and foremost, by the thickness of the peat layer. Drainage intensity also plays a crucial role; annual NNM tends to be lower in poorly drained soils than in well-drained soils (Ullah and Moore 2009). In the present case, the peat layer was quite thin, having attained a thickness of only up to 45 cm after the almost 50-year drainage period. Similar or even lower values of NNM in pine stands (6–24 kg ha^{-1} yr^{-1}) have been reported earlier from Estonia (Pajuste and Frey 2003; Külla et al. 2004). In a study from Sweden, negative N mineralization occurred in pine stands growing on sandy soils (Vestgarden et al. 2003).

The share of net nitrification and net ammonification processes at the studied sites was different, which can be explained by soil fertility and reaction. It is known that low pH restricts nitrification and almost no nitrification can be detected at pH < 4 (Persson and Wiren 1995); in the studied pine stand average pH was 2.6. (Table 2). When in the birch and spruce stands nitrification was the dominating process, then in the pine stand ammonification was prevailing. The NNM flux in the pine stand was also strongly affected by litter quality. It was estimated that about 10 kg of N reached the soil annually through litterfall, which was about three times lower than in the birch and spruce stands. The NNM flux is clearly affected by the litter C/N ratio as for the pine stand the litter C/N ratio was the highest among the studied stands.

5 Conclusion

In the studied drained peatlands, the annual net nitrogen mineralization (NNM) flux was largely influenced by the post-drainage peatland type and the tree species of stand. The annual NNM flux was large in fertile full-drained eutrophic swamps; it was lower in the spruce stand (87.7 kg N ha^{-1} yr^{-1}) than in the downy birch stand (127.5 kg N ha^{-1} yr^{-1}); this difference was related to the quality of aboveground litter. Thus both N content and the litter C/N ratio are important indicators of litter affecting NNM.

The annual NNM flux in the pine stand growing in a full-drained transitional bog was significantly smaller (11.8 kg N ha^{-1} yr^{-1}), which was due to the co-effect of the soil and the ree species.

Myrtillus full-drained swamp has evolved from transitional bog after long-term intensive drainage, but soil fertility and especially soil N content in the peat soil of transitional bog are significantly lower compared with eutrophic swamp. Moreover, N content is much lower in the needle litter of Scots pine than in the birch leaves or spruce needles.

The nitrification process was limited by soil pH: nitrification was dominating in the fertile drained peat soil with higher pH and N content, whereas ammonification dominated in the pine stand in low-fertility drained transitional bog. The high NNM rate indicates that drained peat soils can be as fertile as mineral soils, while the NNM flux depends in turn largely on soil properties and on tree species.

Acknowledgements

The research project "Carbon and nitrogen cycle in drained forests" (2013–2016), based of which the current study was completed, was supported by the State Forest Management Centre of Estonia No 1-18/113. The research was also supported by the Ministry of Education and Research of Estonia (grants IUT21-04 and IUT2-16); and the EU through European Regional Development Fund project BioAtmos (3.2.0802.11-0043) and Centres of Excellence ENVIRON and EcolChange. Also by the project of the Estonian University of Life Sciences T170053MIMK as well as by the Environmental Investment Centre project No. 5725. We thank Mrs. Ester Jaigma for revising the English text of the manuscript.

References

Aber J.D., Nadelhoffer J.K., Steudler P., Melillo J.M. (1989). Nitrogen saturation in Northern forest ecosystems. BioScience 39(6): 378–386. https://doi.org/10.2307/1311067.

Adams M.A., Polglase P.J., Attiwill M.P., Weston C.J. (1989). *In situ* studies on nitrogen mineralization and uptake in forest soils: some comments on methodology. Soil Biology and Biochemistry 21(39): 423–429. https://doi.org/10.1016/0038-0717(89)90154-5.

Ahti T., Hämet-Ahti L., Jalas J. (1968). Vegetation zones and their sections in north-western Europe. Annales Botanici Fennici 5: 169–211.

Andersson P., Berggren D., Nilsson I. (2002). Indices for nitrogen status and nitrate leaching from Norway spruce (*Picea abies* (L.) Karst.) stands in Sweden. Forest Ecology and Management 157(1–3): 39–53. https://doi.org/10.1016/S0378-1127(00)00651-4.

Aosaar J., Varik M., Lõhmus K., Ostonen I., Becker H., Uri V. (2013). Long-term study of above- and below-ground biomass production in relation to nitrogen and carbon accumulation dynamics in a grey alder (*Alnus incana* (L.) Moench) plantation on former agricultural land. European Journal of Forest Research 132(5–6): 737–749. https://doi.org/10.1007/s10342-013-0706-1.

Baldock J.A., Nelson P.N. (2000). Soil organic matter. In: Sumner M.E. (eds.). Handbook of soil science. CRC Press LLC, Boca Raton, USA. B25-B84.

Becker H., Aosaar J., Varik M., Morozov G., Kanal A., Uri V. (2016). The effect of Norway spruce stump harvesting on net nitrogen mineralization and nutrient leaching. Forest Ecolology and Management 377: 150–160. https://doi.org/10.1016/j.foreco.2016.07.005.

Becker H., Uri V., Aosaar J., Varik M., Mander Ü., Soosaar K., Hansen R., Teemusk A., Morozov G., Kutti S., Lõhmus K. (2015). The effects of clear-cut on net nitrogen mineralization and nitrogen losses in a grey alder stand. Ecological Engineering 85: 237–246. https://doi.org/10.1016/j.ecoleng.2015.10.006.

Birdsey R., Pan Y. (2015). Trends in management of the world's forests and impacts on carbon stocks. Forest Ecology and Management 355: 83–90. https://doi.org/10.1016/j.foreco.2015.04.031.

Cools N., Vesterdal L., De Vos B., Vanguelova E., Hansen K. (2014). Tree species is the major factor explaining C:N ratios in European forest soils. Forest Ecology and Management 311: 3–16. https://doi.org/10.1016/j.foreco.2013.06.047.

Connell M.R., Raison R.J., Khanna P.K. (1995). Nitrogen mineralization in relation to site history and soil properties in a range of Australian forest soils. Biology and Fertility of Soils 20(4): 213–220. https://doi.org/10.1007/BF00336080.

Cotrufo M.F., Ineson P., Roberts J.D. (1995). Decomposition of leaf litters with varying C-to-N ratios. Soil Biology and Biochemistry 27(9): 1219–1221. https://doi.org/10.1007/BF00336080.

Duran J., Morse J.L., Groffman P.M. (2012). Comparison of in situ methods to measure N mineralization rates in forest soils. Soil Biology and Biochemistry 46: 145–147. https://doi.org/10.1016/j.soilbio.2011.12.005.

Eno C.F. (1960). Nitrate production in the field by incubating the soil in polyethylenebags. In: Proceedings of the Soil Science Society of America 24(4): 277–279. https://doi.org/10.2136/sssaj1960.03615995002400040019x.

FAO (2006). World reference base for soil resources. A framework for International classification, correlation, and communication. Rome. 128 p.

Glina B., Bogacz A., Woźniczka P. (2016). Nitrogen mineralization in forestry-drained peatland soils in the Stołowe Mountains National Park (Central Sudetes Mts). Soil Science Annual 67(2): 64–72. https://doi.org/10.1515/ssa-2016-0009.

Goodale C.L., Aber J.D. (2001). The long term effects of land-use history on nitrogen cycling in northern hardwood forests. Ecological Applications 11: 253–267. https://doi.org/10.1890/1051-0761(2001)011%5B0253:TLTEOL%5D2.0.CO;2.

Gundersen P. (1995). Impacts of nitrogen deposition: scientific background. In: Forsius M., Kleemola S. (eds.). Fourth Annual Synoptic Report, Helsinki. p. 9–18.

Hanselman T.A., Graetz D.A., Obreza T.A. (2004). A comparison of in situ methods for measuring net nitrogen mineralization rates of organic soil amendments. Journal of Environmental Quality 33(3): 1098–1105. https://doi.org/10.2134/jeq2004.1098.

Hargreaves K.J., Milne R., Cannell M.G.R. (2003). Carbon balance of afforested peatland in Scotland. Forestry 76(3): 299–317. https://doi.org/10.1093/forestry/76.3.299.

Helmisaari H.-S. (1995). Nutrient cycling in *Pinus sylvestris* stand in eastern Finland. Plant and Soil 168(1): 327–336. https://doi.org/10.1007/BF00029345.

Helmisaari H.-S., Makkonen K., Kellomäki S., Valtonen E., Mälkonen E. (2002). Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. Forest Ecology and Management 165(1–3): 317–326. https://doi.org/10.1016/S0378-1127(01)00648-X.

Korjus H., Põllumäe P., Kangur A. (2015). Why do we need a research and demonstration area of forest management planning at Järvselja? Forestry Studies 63: 151–159.

Kupper P., Sõber J., Sellin A., Lõhmus K., Tullus A., Räim O., Lubenets K., Tulva I. Uri V. Zobel M., Kull O., Sõber A. (2011). An experimental facility for free air humidity manipulation (FAHM) can alter water flux through deciduous tree canopy. Environmental and Experimental Botany 72(3): 432–438. https://doi.org/10.1016/j.envexpbot.2010.09.003.

Külla T., Lõhmus K., Kurvits V., Seemen H. (2004). *In situ* net nitrogen mineralisation in the organic layer under a middle-aged Rhodococcum Scots pine (*Pinus sylvestris* (L.) stand on podzol. Forestry Studies 40: 176–186.

Laine J., Vasander H., Sallantaus T. (1995). Ecological effects of peatland drainage for forestry. Environmental Review 3(3–4): 286–303. https://doi.org/10.1139/a95-015.

Lovett G.M., Weathers K.C., Arthur M.A. (2002). Control of nitrogen loss from forested watersheds by soil carbon:nitrogen ratio and tree species composition. Ecosystems 5(7): 712–718. https://doi.org/10.1007/s10021-002-0153-1.

Lovett G.M., Weathers K.C., Arthur M.A., Schultz J.C. (2004). Nitrogen cycling in a northern hardwood forest: do species matter? Biochemistry 67(3): 289–308. https://doi.org/10.1023/B:BIOG.0000015786.65466.f5.

Luo Y., Su B., Currie W.S., Dukes J.S., Finzi A., Hartwig A., Hungate B., McMurtrie R.E., Oren R., Parton W.J., Pataki D.E., Shaw M.R., Zak D.R., Field C.B. (2004). Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. Bioscience 54(8): 731–739. https://doi.org/10.1641/0006-3568(2004)054%5B0731:PNLOER%5D2.0.CO;2.

Lõhmus K., Kuusemets V., Ivask M., Teiter S., Augustin J., Mander Ü. (2002). Budgets of nitrogen fluxes in riparian grey alder forests. Archive für Hydrobiologie 13(3–4): 321–332. https://doi.org/10.1127/lr/13/2002/321.

Lõhmus K., Truu M., Truu J., Ostonen I., Kaar E., Vares A., Uri V., Alama S., Kanal A. (2006). Functional diversity of culturable bacterial communities in the rhizosphere in relation to fine-root and soil parameters in alder stands on forest, abandoned agricultural, and oil-shale areas. Plant and Soil 283(1–2): 1–10. https://doi.org/10.1007/s11104-005-2509-8.

Maag M., Vinther F.P. (1996). Nitrous oxide emission by nitrification and denitrification in different soil types and at different soil moisture contents and temperatures. Applied Soil Ecology 4(1): 5–14. https://doi.org/10.1016/0929-1393(96)00106-0.

Magill A.H., Aber J.D., Berntso G.M., McDowell W.H., Nadelhoffer K.J., Melillo J.M., Staudler P. (2000). Long-term nitrogen additions and nitrogen saturation in two temperate forests. Ecosystems 3(3): 238–253. https://doi.org/10.1007/s100210000023.

Martikainen P.J., Nykänen H., Grill P., Silvola J. (1993). Effect of a lowered water table on nitrous oxide fluxes from northern peatlands. Nature 366: 51–53. https://doi.org/10.1038/366051a0.

McClaugherty C.A., Pastor J., Aber J.D., Melillo J.M. (1985). Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66(1): 266–275. https://doi.org/10.2307/1941327.

Meyer A., Tarvainen L., Nousratpour A., Björk R.G., Ernfors M., Grelle A., Kasimir Klemedtsson Å., Lindroth A., Räntfors M., Rütting T., Wallin G., Weslien P., Klemedtsson L. (2013). A fertile peatland forest does not constitute a major greenhouse gas sink. Biogeosciences 10: 7739–7758. https://doi.org/10.5194/bg-10-7739-2013.

Millard P., Sommerkorn M., Grelet G.-A. (2007). Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal. New Phytology 175(1): 11–28. https://doi.org/10.1111/j.1469-8137.2007.02079.x.

Minkkinen K., Korhonen R., Savolainen I., Laine J., (2002). Carbon balance and radiative forcing of Finnish peatlands 1900–2100 – the impact of forestry drainage. Global Change Biology 8(8): 785–799. https://doi.org/10.1046/j.1365-2486.2002.00504.x.

Nadelhoffer K.J., Aber J.D., Melillo J.M. (1984). Seasonal patterns of ammonium and nitrate uptake in nine temperate forest ecosystems. Plant and Soil 80(3): 321–335. https://doi.org/10.1007/BF02140039.

Ojanen P., Minkkinen K., Penttilä T. (2013). The current greenhouse gas impact of forestry-drained boreal peatlands. Forest Ecolology and Management 289: 201–208. https://doi.org/10.1016/j.foreco.2012.10.008.

Paavilainen E., Päivänen J. (1995). Peatland forestry: ecology and principles Ecological studies 111. Springer, Berlin. https://doi.org/10.1007/978-3-662-03125-4.

Pajuste K., Frey J. (2003). Nitrogen mineralisation in podzol soils under boreal Scots pine and Norway spruce stands. Plant and Soil 257(1): 237–247. https://doi.org/10.1023/A:1026222831694.

Peltomaa R. (2007). Drainage of forests in Finland. Irrigation and Drainage 56(1): 151–159. https://doi.org/10.1002/ird.334.

Persson T., Wirén A. (1995). Nitrogen mineralization and potential nitrification at different depths in acid forest soils. Plant and Soil 168(1): 55–65. https://doi.org/10.1007/BF00029313.

Raison R.J., Conell M.J., Khanna P.K. (1987). Methodology for studying fluxes of soil mineral-N *in situ*. Soil Biology and Biochemistry 19(5): 521–530. https://doi.org/10.1016/0038-0717(87)90094-0.

Scott A.N., Binkley D. (1997). Foliage litter quality and annual net N mineralization: comparison across North American forest sites. Oecologia 111(2): 151–159. https://doi.org/10.1007/s004420050219.

Silins U., Rothwell R.L. (1999). Spatial patterns of aerobic limit depth and oxygen diffusion rate at two peatlands drained for forestry in Alberta. Canadian Journal of Forest Research 29(1): 53–61. https://doi.org/10.1139/x98-179.

Silvola J., Alm J., Ahlholm U., Nykanen H., Martikainen P.J. (1996). CO_2 fluxes from peat in boreal mires under varying temperature and moisture conditions. Journal of Ecology 84(2): 219–228. https://doi.org/10.2307/2261357.

Stenger R., Priesack E., Beese F. (1995). Rates of net nitrogen mineralization in disturbed and undisturbed soils. Plant and Soil 171(2): 323–332. https://doi.org/10.1007/BF00010288.

Tate R.L. (1995). Soil microbiology. John Wiley & Sons, Inc, New York. 398 p.

Tietema A., Riemer L., Verstraten J.M., van der Maas M.P., van Wijk A.J., van Voorthuyzen I. (1993). Nitrogen cycling in acid forest soils subject to increased atmospheric input. Forest Ecology and Management 57(1–4): 29–44. https://doi.org/10.1016/0378-1127(93)90160-O.

Tietema A., Verstraten J.M. (1992). Nitrate cycling in an acid forest ecosystem in the Netherlands under increased atmospheric nitrogen input. Biogeochemistry 15: 21–46.

Ullah S., Moore T.R. (2009). Soil drainage and vegetation controls of nitrogen transformation rates in forest soils, southern Quebec. Journal of Geophysical Research: Biogeosciences 114: G01014. https://doi.org/10.1029/2008JG000824.

Uri V., Aosaar J., Varik M., Becker H., Kukumägi M., Ligi K., Pärn L., Kanal A. (2015). Biomass resource and environmental effects of Norway Spruce (*Picea abies*): an Estonian case study. Forest Ecology and Management 335: 207–215. https://doi.org/10.1016/j.foreco.2014.10.003.

Uri V., Aosaar J., Varik M., Becker H., Ligi K., Padari A., Kanal A., Lõhmus K. (2014). The dynamics of biomass production, carbon and nitrogen accumulation in grey alder (*Alnus incana* (L.) Moench) chronosequence stands in Estonia. Forest Ecology and Management 327: 106–117. https://doi.org/10.1016/j.foreco.2014.04.040.

Uri V., Lõhmus K., Kiviste A., Aosaar J. (2009). The dynamics of biomass production in relation to foliar and root traits in a grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural land. Forestry 82(1): 61–74. https://doi.org/10.1093/forestry/cpn040.

Uri V., Lõhmus K., Kund M., Tullus H. (2008). The effect of land use on net nitrogen mineralization on abandoned agricultural land: silver birch stand versus grassland. Forest Ecolology and Management 255(1): 226–233. https://doi.org/10.1016/j.foreco.2007.09.019.

Uri V., Lõhmus K., Mander Ü., Ostonen I., Aosaar J., Maddisson M., Helmisaari H.-S., Augustin J. (2011). Long-term effects on nitrogen budget of a short-rotation grey alder (*Alnus incana* (L.) Moench) forest in abandoned agricultural land. Ecological Engineering 37(6): 920–930. https://doi.org/10.1016/j.ecoleng.2011.01.016.

Uri V., Lõhmus K., Tullus H. (2003). Annual net nitrogen mineralization in a grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural land. Forest Ecology and Management 184(1–3): 167–176. https://doi.org/10.1016/S0378-1127(03)00210-X.

Uri V., Kukumägi M., Aosaar J., Varik M., Becker H., Morozov G., Karoles K. (2017). Ecosystems

carbon budgets of differently aged downy birch stands growing on well-drained peatlands. Forest Ecology and Management 399: 82–93. https://doi.org/10.1016/j.foreco.2017.05.023.

Van Praag H.J., Weissen F. (1973). Elements of a functional definition of oligotrophic humus based on the nitrogen nutrition of forest stands. Journal of Applied Ecology 10(2): 569–583. https://doi.org/10.2307/2402302.

Varik M., Aosaar J., Ostonen I., Lõhmus K., Uri V. (2013). Carbon and nitrogen accumulation in belowground tree biomass in a chronosequence of silver birch stands. Forest Ecology and Management 302: 62–70. https://doi.org/10.1016/j.foreco.2013.03.033.

Varik M., Kukumägi M., Aosaar J., Becker H., Ostonen I., Lõhmus K., Uri V. (2015). Carbon budgets in fertile silver birch (*Betula pendula* Roth) chronosequence stands. Ecological Engineering 77: 284–296. https://doi.org/10.1016/j.ecoleng.2015.01.041.

Vestgarden L.S., Selle L.T., Stuanes A.O. (2003). *In situ* soil nitrogen mineralization in a Scots pine (*Pinus sylvestris* L.) stand: effects of increased nitrogen input. Forest Ecology and Management 176(1–3): 205–216. https://doi.org/10.1016/S0378-1127(02)00275-X.

Wang M., Talbot J., Moore T.R. (2018) Drainage and fertilization effects on nutrient availability in and ombrotrophic peatland. Sceiance of the Total Environment 621: 1255–1263. https://doi.org/10.1016/j.scitotenv.2017.10.103.

Westman C.J., Laiho R. (2003). Nutrient dynamics of drained peatland forests. Biogeochemistry 63(3): 269–298. https://doi.org/10.1023/A:1023348806857.

Yearbook Forest 2016 (2017). Aastaraamat Mets 2016. Keskkonnateabe Keskus, Tartu. [In Estonian].

Zak D.R., Grigal D.R., Gleeson S., Tilman D. (1990). Carbon and nitrogen cycling during old-field succession: constraints on plant and microbial biomass. Biochemistry 11(2): 111–129. https://doi.org/10.1007/BF00002062.

Total of 68 references.

III

Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., Soosaar, K., **Morozov, G.**, Ligi, K., Padari, A., Ostonen, I., Karoles, K. (2017). Carbon budgets in fertile grey alder (*Alnus incana* (L.) Moench.) stands of different ages. Forest Ecology and Management, 396: 55−67.

Forest Ecology and Management 396 (2017) 55–67

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Carbon budgets in fertile grey alder (*Alnus incana* (L.) Moench.) stands of different ages

V. Uri [a,*], M. Kukumägi [b], J. Aosaar [a], M. Varik [a], H. Becker [a], K. Soosaar [b], G. Morozov [a], K. Ligi [a], A. Padari [a], I. Ostonen [b], K. Karoles [a]

[a] Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, 51014 Tartu, Estonia
[b] Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia

ARTICLE INFO

Article history:
Received 11 November 2016
Received in revised form 3 April 2017
Accepted 5 April 2017

Keywords:
Grey alder
Net ecosystem production
Soil respiration
Carbon fluxes
Biomass
Land use history

ABSTRACT

Estimation of the carbon (C) storages and fluxes in different forest ecosystems is essential for understanding their C sequestration ability. Grey alder (*Alnus incana* (L.) Moench) is a fast growing tree species with a great potential for short-rotation forestry in the Nordic and Baltic countries and its stands are considered C accumulating ecosystems. We hypothesized that grey alder stands growing at fertile sites act as C sinks in the young and middle-age stages, while mature stands become C sources as a consequence of declined net primary production (NPP). Net ecosystem production (NEP) was studied in five grey alder stands aged between 9 and 40 years. It was found that the NEP of the studied grey alder stands of different ages varied from −1.98 to +4.14 t C ha^{-1} yr^{-1}. The oldest grey alder stand proved to be a weak C source (−0.77 t C ha^{-1} yr^{-1}). However, also young alder stands regenerated in a clear-cut area may emit C in the earlier stage, owing to previous cutting and decomposition of organic residues matter. In this aspect, the land use history is of great significance.

Leaf litter accounted for the largest (44–61%) annual organic C input to soil, the fine roots contributed with 12–32% and the herbaceous understorey (aboveground + belowground), with 14–26% to it. Annual cumulative soil heterotrophic respiration (Rh) in the studied stands ranged between 2.6 and 5.8 t C ha^{-1} yr^{-1}; C leaching was negligible, being 10–30 kg C ha^{-1} yr^{-1}. The C sequestration to soil depended on previous land use; in the first forest generation, i.e. a stand growing on previous agricultural land, the annual C_{org} input into soil exceeded Rh, which indicated C accumulation in soil. Although grey alder stands are generally C accumulating ecosystems, the annual biomass production of the studied stands was highly variable; thus annual NEP depended on the effect of the year rather than on stand age. The current study demonstrates that use of repeated time-series measurements applied for stands of different development stages can provide more detailed estimation of C accumulation in forest ecosystems.

1. Introduction

Forests accumulate carbon (C) in plant biomass as well as in soil and the proportion of the respective C storages may be highly variable (Cannell, 1999; Pussinen et al., 2002; Mund et al., 2002; Laiho et al., 2003; Ågren and Hyvönen, 2003; Uri et al., 2012, 2014). Adequate assessment of the dynamics of C accumulation in a forest ecosystem (both tree biomass and soil) requires an integrated approach. When estimation of the C sink in forest trees in relation to their biomass production and this C flux is often based on forest inventory data or on forest growth models, then estimation of C accumulation in soil is more sophisticated as there is few data about C sequestration into soil. Because of the high heterogeneity of forest soils, the cycling and accumulation of C in different forest ecosystems is very variable. As the forests of the hemiboreal region act mostly as C sinks (Dixon et al., 1994; Peng et al., 2008), quantification and modelling of the main C fluxes of different forest ecosystems are highlighted.

Site fertility, composition of tree species and land use history are important factors that affect C accumulation in forests (Uri et al., 2011; Somogyi et al., 2013; Aosaar et al., 2016). *Alnus* species occupy an exceptional position among forest tree species owing to their symbiotic nitrogen (N) fixation ability of the bacteria *Frankia* (Benson, 1982). The effect of N_2 fixing trees on the soil C pool may be more marked since N and C cycling are strongly interrelated in forest ecosystems (Binkley, 2005).

* Corresponding author.
E-mail address: veiko.uri@emu.ee (V. Uri).

http://dx.doi.org/10.1016/j.foreco.2017.04.004
0378-1127/

Table 1
The main characteristics of the studied grey alder stands: A – stand age, N – stand density, $D_{1.3}$ – average diameter at breast height, H – average height, BA – basal area (Uri et al., 2014).

Stand	Age class	Origin	A[a] (year)	N (trees ha^{-1})	$D_{1.3}$ (cm)	H (m)	BA (m^2 ha^{-1})
Kolleste 1	Young	Sprout	7	18,750	3.0	6.5	13.3
Ilmatsalu	Middle-aged	Sprout	17	4630	7.3	11.2	19.5
Voopste	Middle-aged	Sprout	21	3280	9.5	14.3	23.1
Agali	Mature	Seed	32	1528	15.4	17.3	28.5
Kolleste 2	Mature	Seed	38	2734	15.2	18.0	49.5

[a] Stand age at the beginning of the study (2011).

According to the Paris Agreement 2015, governments should significantly reduce the use of fossil fuels and increase the share of bioenergy in the nearest future. This will probably increase the demand for various bioenergy sources and may intensify the management of forests. In this aspect, grey alder is a prospective fast growing tree species for short-rotation forestry (SRF) in Estonia (Uri et al., 2002, 2003, 2009, 2011) as well as in the other Nordic and Baltic countries (Granhall and Verwijst, 1994; Saarsalmi, 1995; Rytter, 1996; Telenius, 1999; Miežite, 2008; Hytönen and Saarsalmi, 2009; Aosaar et al., 2012; Hytönen and Saarsalmi, 2015; Rytter and Rytter, 2016). It is evident that the need for understanding of the functioning of these forests is growing.

Studies of C budgets on the ecosystem's scale are important for understanding the driving forces behind the functioning of the C cycle and C sequestration capacity (Fang et al., 2007). However, relevant studies addressing alders are still limited. Recent results have demonstrated that grey alder stands are able to accumulate a considerable amount of C both in biomass and soil during a relatively short time period (Uri et al., 2011, 2014; Aosaar et al., 2013; Rytter and Rytter, 2016). In this respect, soil heterotrophic respiration (Rh) as the main C output flux from forest ecosystems plays a crucial role. However, only a few results are available about soil respiration in grey alder stands (Soosaar et al., 2011).

The main aim of the present study was to estimate net ecosystem production (NEP) in five grey alder stands of different ages growing on fertile soils, by using C budgeting. We hypothesized that the C accumulation ability of grey alder stands is higher in young stands and will decrease in mature stands. In the study we used repeated annual measurements of different C fluxes in five consecutive years for stands of different ages. This approach will minimise the effect of fluctuating weather conditions in different years and can hence provide more reliable results about the annual growth of trees and NEP, which indicates net C sink or C emission between the atmosphere and forest.

The specific aims of the study were:

- to estimate the dynamics of the biomass production of grey alder stands of different ages growing on fertile soils in five consecutive years;
- to assess the biomass, production and turnover rate of fine roots in a grey alder stands of different ages;
- to estimate and analyse differences in total soil respiration and in the heterotrophic respiration fluxes in a grey alder stands of different ages.

2. Material and methods

2.1. Site description

Five naturally regenerated pure grey alder stands located in Southern Estonia, which belonged to different age classes, were included in the study (Table 1). The Kolleste 1, Ilmatsalu and Voopste stands were regenerated by sprouts; Agali and Kolleste 2 were seed originated. The selected stands were also used in our earlier extensive study (Uri et al., 2014). However, the main stand and soil characteristics and the modified names of the stands are presented as relevant background data (Tables 1 and 2). Based on the biological age of the trees, we classified Kolleste 1 as a young stand, Ilmatsalu and Voopste, as middle-aged stands, and Agali and Kolleste 2, as mature stands.

All studied stands grew in the *Oxalis* or the *Aegopodium* site type according to the Estonian classification (Lõhmus, 1984). *Aegopodium* is the most fertile site type in Estonian forests with high soil nutrient content and a favourable water table (Lõhmus, 1984). The soils of the *Oxalis* site type are also highly productive owing to the thick humus (A) layer, optimal moisture conditions for plant growth and fast litter decomposition (Table 2).

The previous land use of the sites was different: long-standing forest land (Kolleste 1, Ilmatsalu and Voopste stands) and abandoned agricultural land (Agali stand) (Table 2). The previous land use of Kolleste 2 is not clear, most probably, this stand has formed on previous grassland. All stands were unmanaged, which is typical for grey alder stands in Estonia.

2.2. Estimation of the biomass and production of stand

2.2.1. Aboveground leafless biomass of stand

2.2.1.1. Biomass and production of the trees. The leafless aboveground biomass and current-year production of the trees was estimated in September 2011 when the process of biomass formation was completed; the method of model trees (Uri et al., 2011, 2012, 2014) was used. For this, a sample plot (at 0.02–0.075 ha) was established in each stand. All trees growing in the sample plot were numbered and breast height diameter ($D_{1.3}$) of each single tree was measured annually. Additional 10–15 trees were measured for height to estimate average stand height.

The trees were divided into five classes on the basis of $D_{1.3}$, and a model tree was selected randomly from each class. Altogether 6 model trees were felled per study area. The model trees were fractioned (Uri et al., 2014) and from every fraction, a subsample was taken for estimation of dry matter content as well as for chemical analysis (see Section 2.7).

The aboveground leafless biomass of the stands for 2011 was estimated on the basis of an allometric model (Uri et al., 2014). To estimate the leafless aboveground biomass of the trees for 2012–2015, the diameter of the trees in the sample plots was measured annually in autumn and for calculation of stem mass, a general model for Estonian grey alder stands (Uri et al., 2014) was applied. The current annual production (CAP) of stem mass for 2012–2015 was calculated as the difference between the stem masses for the studied year and the stem masses for the previous year.

The biomass of the branches was estimated by their percentage distribution on the basis of the model trees and the production of the current-year shoots was assumed to be equal to their biomass (Uri et al., 2011). The production of the leaves was found on the basis of annual leaf litter (see Section 2.3).

To compare the growth dynamics of the studied stands by means of the general growth model for Estonian grey alder stands

Table 2
The soil characteristics and soil types of the studied stands. N - Kjeldahl nitrogen (%), P - available (AL) phosphorus (mg kg^{-1}), K – available (AL) potassium (mg kg^{-1}), OM - organic matter content (%), BD - bulk density (g cm^{-3}). Presented average concentrations and bulk density represent the upper 10 cm soil layer. C – carbon storage (t ha^{-1}) (upper 0–30 cm soil layer).

	N	P	K	pH_{KCl}	C:N ratio	OM	BD	C	Site history	Soil type
Kolleste 1	0.45	7.8	79.1	5.0	14.1	10.9	0.80	178.3	Forest land	*Umbric Gleysol*
Ilmatsalu	0.47	20.9	93.7	5.7	13.0	10.6	0.98	119.2	Forest land	*Endogleyic Cambisol*
Voopste	0.36	8.3	55.0	4.5	14.0	8.6	0.76	104.5	Forest land	*Endogleyic Arenosol*
Agali	0.36	9.4	59.1	5.9	11.9	7.5	1.00	107.3	Agricultural land	*Umbric Planosol*
Kolleste 2	0.32	4.3	73.2	3.7	13.3	7.2	0.93	82.5	Grassland	*Gleyic Podzol*

Table 3
The parameter (a_1) and characteristics of the growth model (1) of the studied stands.

Stand	a_1	Standard error	t-value	P-value
Kolleste 1	6.087	0.139	0.861	0.393
Ilmatsalu	5.764	0.137	−1.484	0.144
Voopste	5.886	0.138	−0.587	0.560
Agali	6.023	0.140	0.401	0.690
Kolleste 2*	6.479	0.141	3.638	0.001*

* Significant difference from the values of the yield table.

(Uri et al., 2014), the modelling approach was used (Naslund function (1) (Schmidt et al., 2011)). Both the data of five-year measurements and the biomass data from our previous study (Uri et al., 2014) were used for prediction of the dynamics of stand growth.

$$V = \exp a_1 \cdot \left(\frac{A}{A+3}\right)^{5.387} \quad (1)$$

where

V is stem volume of stand; A is stand age in years and a_1 is a specific stand parameter (Table 3).

2.2.1.2. Biomass and production of herbaceous plants. From each study site, ten random samples over the whole stand were taken in the middle of July 2013 when aboveground biomass was assumed to be at maximum. Additionally, at two sites (Agali and Voopste) this procedure was carried out also in 2012 and 2014. The aboveground part of all ground vegetation was collected from a 0.5 m^2 quadrate and weighed to 0.1 g. Subsamples were taken for estimation of dry matter content and C concentration. The subsamples were dried at 70 °C to constant weight and weighed to 0.01 g. As the aboveground part of herbs is annual, aboveground production was assumed to be equal to biomass.

2.2.2. Below-ground biomass and production

2.2.2.1. Coarse root biomass and production of alders. The average proportion of belowground biomass, i.e. 19.5% of aboveground woody biomass, was used to estimate the belowground biomass of the coarse root fraction. This assumption is based on previous studies: a corresponding proportion of 18.5% was estimated for a 10-year-old grey alder stand (Uri et al., 2009) and a slightly higher proportion, 20.3%, was estimated for an older stand (Lõhmus et al., 1996). However, in young deciduous stands, the share of belowground biomass may be higher than in middle-age or matured stands (Varik et al., 2013). We therefore used a higher proportion (23.5%) for the youngest stand (Kolleste 1) according to the data of an earlier study (Uri et al., 2002). Coarse root production was calculated on the basis of the equal relative increments of aboveground woody biomass; the relative increments of the aboveground and belowground woody biomass fractions were assumed to be equal (Uri et al., 2011). Since C concentration did not vary significantly within the coarse roots (Aosaar et al., 2013), we used average C concentration (50%) for calculating C accumulation in course root production.

2.2.2.2. Fine root biomass and production of trees and herbaceous plants. The fine root (d < 2 mm) biomass (FRB) of the alders was estimated using soil cores. In each stand, 20 soil cores were taken randomly all over the stand with a cylindrical soil auger in autumn 2013. To avoid compression of the soil layers, the internal diameter of the upper part of the auger was 1.6 mm larger than the diameter of the cutting edge (48 mm). The soil cores were divided into four layers (0–10; 10–20; 20–30 and 30–40 cm), placed in polyethylene bags and kept in a refrigerator at −5 °C until processing. The fine roots of the alders, as well as the roots of the herbaceous plants were separated from the washed-out samples under a binocular microscope and soil particles were carefully removed. The samples were dried up to 70 °C and weighed to 0.001 g. The biomass of the nodules was not taken account since their share in total belowground biomass is negligible (Saarsalmi et al., 1985; Rytter, 1989; Uri et al., 2002, 2009; Rytter and Rytter, 2016). Soil core data were used for estimation of fine root biomass per hectare, summing up the average values for the successive soil layers in the soil cores.

To assess the C flux to soil through root litter, fine root production (FRP) was estimated by using the root mesh (root inclusion net) method (Hirano et al., 2009; Lukac and Godbold, 2010). In the Agali stand, vertical nylon meshes (mesh size 1.5 mm, width 7 cm and length 20 cm) were installed in soil in autumn 2011. In the other studied stands, this procedure was done one year later (in 2012). The first 25 samples from each stand were taken one year after installation, i.e. in October 2012 and 2013. Next sampling in all stands was carried out in October 2014. Using a spade, a soil block with edges of about 10 cm from both sides of the net and width a height of 20 cm was carefully extracted from soil, placed in a plastic box, packed in a polyethylene bag and transported to the lab. To extract the nets, soil was cut at 1 cm beyond a net with a long-blade knife. The formed soil block was shaken free of soil and the net with the remaining roots was placed in water. The fine roots penetrating the net were washed out and carefully removed. The roots were placed in Petri dishes filled with water and sorted into the living and dead grey alder roots; the remaining roots were considered to belong to understorey plants. The separated roots were dried at 70 °C and weighed.

Fine root turnover rate was calculated by dividing FRP (g m^{-2} $year^{-1}$) by mean fine root biomass (g m^{-2}) according to McClaugherty et al. (1982). Fine root longevity ($year^{-1}$) was calculated as the reciprocal of root turnover rate. For calculation of the C flux into soil through fine root litter, an average C concentration of

50% was used (Aosaar et al., 2013). For the below-ground fraction of the understorey, the turnover rate was assumed to be 1 year (Uri et al., 2011; Varik et al., 2015).

2.3. Estimation of the litter flux

Ten litter traps were placed randomly in each stand in the autumn of 2011 and litter was sampled monthly during the period of 2012–2014. The collecting area of the litter traps was different depending on stand age and density: in Kolleste 1 it was 0.25 m^2; in Ilmatsalu and Voopste, 0.36 m^2; in Agali and Kolleste 2, 0.58 m^2. The collected samples were divided into different fractions: leaves, branches and other material (e.g. seeds, pieces of bark, buds, etc.) and dried at 70 °C. The organic C input flux into soil via litter was calculated by multiplying the oven dry mass of litter by the corresponding C concentration.

2.4. Soil respiration measurements

Soil respiration rates (μmol CO_2 m^{-2} s^{-1}) were measured once a month from May to October 2013 in all studied stands and in 2014 in Kolleste 1, Voopste and Agali stands using the closed dynamic chamber method (PP *Systems* SRC-1 chamber (volume 1170 cm^3, enclosed soil surface area 78 cm^2) with a gas analyser CIRAS-2 (Differential CO_2/H_2O Infrared Gas Analyzers). To distinguish heterotrophic respiration (Rh) from total soil respiration (Rs), the trenching method with insertion of 8 (10 in Kolleste 1) deep PVC cylinders (diameter 20 cm, height 50 cm) to a depth of 40 cm was applied in October 2012. The deep PVC cylinders were placed randomly all over the study plot. The herbaceous vegetation was carefully removed from the inside of the trench with minimum soil disturbance and the trenched plots were kept free of the living vegetation throughout the study. At approximately 50 cm from each deep PVC cylinder (trenched), collars (diameter 10 cm, height 5 cm) for Rs measurement (control) were installed at a depth of ~2–3 cm. Soil temperature (Ts, °C) was measured simultaneously with soil respiration in the control and trenched plots using an attached soil temperature probe STP-1 (PP Systems International, Inc., USA) inserted at a depth of ~5 cm. In addition, soil temperature (model 1425, Technologies, Inc, USA) was measured every hour in each stand and the data was stored with a data logger (WatchDog 1425, Spectrum Technologies, Inc, USA). Volumetric soil moisture (%) was also measured at a depth of ~5 cm using a HH2 Moisture Meter Version 2 (Delta-T Devices Ltd, UK).

An exponential model (2) was used to describe the relationship between Rs (or Rh) and soil temperature at a depth of 5 cm:

$$\mathrm{Rs(or\ Rh)} = ae^{bTs} \quad (2)$$

where a and b are fitted parameters, and Ts is soil temperature (°C).

Individual models were developed for each stand and for both growing seasons (May–October 2013 and 2014). The cumulative Rs and Rh fluxes for the snow-free period (May–November) were modelled (Eq. (2)) for each stand using the Ts values from the data loggers. The cumulative Rh flux was corrected for the increased decomposition of the severed fine roots and for the lack of fresh inputs of intact roots, caused by trenching (Varik et al., 2015) because decomposition of cut roots and lack of fresh root inputs can modify Rh (Epron, 2009). An approximate decay constant k of 0.20 $year^{-1}$ was used (unpublished data of K. Lõhmus). Since we did not measure the respiration fluxes from December to April, we increased the total value by 10% to calculate the total annual cumulative flux (V. Uri, personal communication). To test the effect of soil moisture on Rs (or Rh), a multilinear regression, where temperature and moisture were the two independent variables, was conducted. Furthermore, Pearson's coefficient of correlation between Rs and soil moisture was calculated and to discard the confounding effect of Ts, partial correlation analysis was used.

2.5. Carbon leaching

The C leaching was estimated by using plate lysimeters (stainless steel; collecting area 627 cm^2) which were randomly installed in soil to a depth of 40 cm in the Agali and Voopste stands in spring 2011. Polyethylene tubes connected the lysimeters to water collectors (6000 ml polyethylene canisters disposed at a depth of 1 m). Water from the canisters was sampled monthly from May 2011 to November 2014 (up to the freezing of soil), through a plastic pipe, using a peristaltic vacuum pump. In the present study, data from 2013 to 2014 were used. The leaching flux of carbon was calculated separately for every sampled month on the basis of the amount of percolated water (10 lysimeters per stand) and the nutrient concentrations analysed from the water samples. The annual cumulative leaching flux was calculated by summing the leaching fluxes in different months.

2.6. Carbon budgeting

The C budgets for all studied stands were compiled by balancing the data of the C input and C output. We used a well-known approach for defining net ecosystem production (NEP), which is the difference between net primary production (NPP) and ecosystem respiration (Lovett et al., 2006). The NEP presents the rate at which C is accumulated in the ecosystem, and is the main parameter characterizing the forest C sink (Chapin et al., 2006; Waring and Running, 2007). The NPP was calculated by summing the annual increments of the aboveground ecosystem compartments (trees, understorey) and the annual increments of the belowground ecosystem compartments (coarse root system, fine roots, roots of the herbaceous understorey). The estimate for NEP was obtained by subtracting heterotrophic respiration (Rh) and leaching (L) from NPP (3) (Clark et al., 2001; Lovett et al., 2006; Meyer et al., 2013):

$$\mathrm{NEP} = \mathrm{NPP} - (\mathrm{Rh} + \mathrm{L}) \quad (3)$$

The C leaching flux was estimated for two study stands (Section 2.5). However, this output flux is usually ignored in C budgeting since its values are negligible. A positive value of NEP indicates the net transfer of C from the atmosphere to forest when the ecosystem acts as a C sink. A negative value of NEP implies the net transfer of C from forest to the atmosphere when the ecosystem is a C source.

2.7. Soil and biomass sampling for chemical analysis

In all studied stands one soil pit (depth 1.0 m) was dug; the soil profile was described and the soil type was determined (Table 2) according to the WRB (2006) (Uri et al., 2014). From every fraction (current year shoots, branches, stemwood and stembark) of the model trees, a subsample was taken for estimation of C concentration. Samples were collected from 3 model trees whose diameter was close to average $D_{1.3}$. Samples of stemwood and stembark were taken from different heights of the model trees (D_0; $D_{1.3}$ and $D_{1/2}$) and pooled proportionately to form a composite sample. The soil C storage and nutrient concentrations as well as the C concentrations in tree biomass were estimated in the course of an earlier study (Uri et al., 2014). To analyse the plant material for C content and for soil C_{org} in the oven-dried samples, the dry combustion method was used with a varioMAX CNS elemental analyser (ELEMENTAR, Germany). For testing N (Kjeldahl) in the soil samples, the Tecator ASN 3313 was employed. Available P and K were extracted with ammonium lactate (0.1 *M* NH4CH3CH(OH)COO–187 + 0.4*M* CH3COOH, pH 3.75). Available phosphorus in the

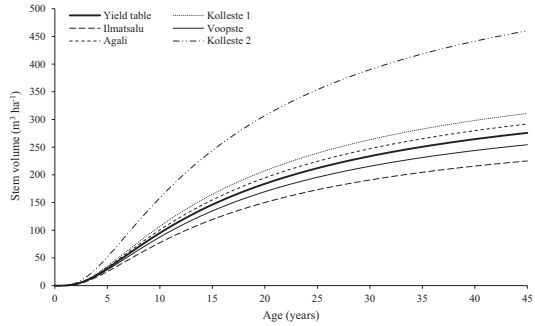


Fig. 1. The dynamics of stem volume in the studied time-series stands in comparison with the Estonian grey alder yield table (Uri et al., 2014).

extraction solution was determined by flow injection analysis with the use of the Tecator ASTN 9/84 and the content of available potassium was determined from the same solution by the flame photometric method.

The analyses were carried out at the Biochemistry Laboratory of the Estonian University of Life Sciences. Water samples were analysed for total organic carbon (TOC) at the Laboratory of the Estonian Environmental Research Ltd using standard methods for water research (APHA 1989).

2.8. Statistical methods

Normality of variables was checked by Lilliefors' and Shapiro-Wilk's tests. The *t*-test for independent samples by groups was employed to compare the herbaceous understorey biomass of different stands. The LSD test was applied for comparison of the litter C flux or soil C content for stands of different ages.

Soil respiration data were normalised by log-transformation. To examine the effect of stand age and treatment (trenching) on Rs (or Rh), Ts and SWC, a repeated measure analysis of variance (ANOVA) was performed using the general linear model (GLM) procedure. In the case of significant effects ($P < 0.05$), means were compared with Tukey's HSD test.

Linear and allometric models were employed for estimating relationships. The measure of the fit of the models was based on the coefficient of determination (R^2) and level of probability (p). In all cases the level of significance $\alpha = 0.05$ was accepted. The softwares STATISTICA 13.0 and R (Crawley, 2007) were employed.

3. Results

3.1. Woody biomass production and carbon accumulation in woody tissues

The general growth dynamics of the studied stands was in good accordance with the data of the Estonian grey alder yield table (Uri et al., 2014). Only the oldest mature stand (Kolleste 2) did demonstrate exceptionally high annual stem mass production, which significantly exceeded the corresponding values of the yield table (Fig. 1, Table 3). Current annual woody biomass production (CAP) in all studied stands fluctuated significantly between the study years, which was probably caused by weather conditions. Comparison of leafless CAP across all stands revealed that it was higher in 2011 and 2014 than in 2013 and 2015 (Table 4).

3.2. Aboveground litter production and its carbon input to soil

The main share of annual aboveground litter was formed of leaf litter (Table 5). The share of the branches was negligible in the youngest stand: ca 1% in all studied years. In the other stands it varied from 2% to 15%. The total annual C flux to soil via litter fall was smaller in the youngest stand but the difference was not statistically significant (LSD test; $P = 0.07$) (Table 5).

3.3. Herbaceous understorey

The aboveground biomass of the herbaceous plants was not dependent on either stand age or density, varying from 0.7 to 1.1 t ha^{-1} in 2013 (Table 6). However, the aboveground biomass of the herbaceous vegetation in the Voopste stand in 2013 (1.14 t ha^{-1}) was significantly larger than in the Kolleste 2 and Ilmatsalu stands (*t*-test; $P < 0.05$). The biomass of the belowground part of the herbaceous plants was similar, roughly 0.4 t ha^{-1}, in all stands.

3.4. Carbon input into soil via the fine roots

Although no correlation was found between fine root ($d < 2$ mm) biomass (FRB) and stand age ($P > 0.05$), FRB tended to be lower in younger stands (Table 7). At the same time, FRB per tree increased significantly ($P < 0.05$) with stand age (Fig. 2). The majority of the fine roots (80%) were located in the upper 20 cm topsoil layer in all stands and FRB declined with increasing soil depth. Fine root annual production (FRP) was similar in all stands with the exception of the Agali stand where the current value was almost twice as low, which can be explained by the lower density of this stand (Table 4).

The turnover of the fine roots decreased with the ageing of the stand while the lifespan of the fine roots increased. The mass of the dead fine roots was of the same magnitude in all studied stands, i.e. roughly 0.6 t ha^{-1} (Table 7). Since fine root necromass was almost constant for all stands, the live-dead root ratio increased with stand age. Since for the fine roots, an average C concentration of 50% was used (Aosaar et al., 2013), the annual belowground organic C input into soil via the fine roots ranged between 0.4 and 0.9 t C ha^{-1} yr^{-1} in 2013 (Table 7).

Table 4
The aboveground leafless and belowground biomass, production and dynamics of C accumulation in the studied grey alder stands of different ages. $D_{1.3}$ – average breast height diameter, H – average height, N - number of trees, G - basal area of stand, AGB – aboveground leafless biomass, BGB – belowground biomass; CAP – current annual leafless production.

Year	Age (year)	$D_{1.3}$ (cm)	H (m)	N (trees ha^{-1})	G (m^2 ha^{-1})	Stem mass (t ha^{-1})	AGB (t ha^{-1})	BGB (t ha^{-1})	CAP of stem mass		CAP of total AGB		CAP of BGB		Total C bound (t C ha^{-1} yr^{-1})
									(t ha^{-1} yr^{-1})	(t C ha^{-1} yr^{-1})	(t ha^{-1} yr^{-1})	(t C ha^{-1} yr^{-1})	(t ha^{-1} yr^{-1})	(t C ha^{-1} yr^{-1})	
Kolleste 1															
2011	7	3.0	6.5	18,750	13.3	31.2	35.0	8.2	5.5	2.56	6.91	3.23	1.62	0.81	4.04
2012	8	3.7	7.6	17,083	18.0	34.3	38.4	9.0	3.0	1.41	4.33	2.02	1.02	0.51	2.53
2013	9	4.0	8.4	14,514	18.3	35.3	39.5	9.3	1.0	0.48	2.19	1.02	0.52	0.26	1.27
2014	10	4.8	9.6	10,833	19.4	38.7	43.4	10.2	3.4	1.61	4.93	2.30	1.16	0.58	2.88
2015	11	5.2	9.8	8889	19.1	40.9	45.8	10.8	2.2	1.02	3.61	1.68	0.85	0.42	2.10
Ilmatsalu															
2011	17	7.3	11.2	4634	19.5	50.1	57.6	11.2	3.3	1.54	4.75	2.22	0.93	0.46	2.68
2012	18	8.0	12.5	4098	20.8	54.9	63.1	12.3	4.8	2.25	6.54	3.05	1.27	0.64	3.69
2013	19	8.7	13.3	3561	21.1	56.7	65.1	12.7	1.8	0.84	3.19	1.48	0.62	0.31	1.79
2014	20	9.3	14.3	3463	23.6	61.1	70.2	13.7	4.4	2.06	6.21	2.90	1.21	0.61	3.51
2015	21	9.9	15.0	3073	23.6	63.6	73.0	14.2	2.5	1.15	4.07	1.90	0.79	0.40	2.29
Voopste															
2011	21	9.5	14.3	3280	23.1	68.2	76.1	14.8	4.5	2.09	5.69	2.66	1.11	0.56	3.22
2012	22	10.1	15.1	3160	25.2	71.1	79.2	15.5	2.8	1.32	3.92	1.83	0.76	0.38	2.21
2013	23	10.8	15.7	2787	25.5	73.8	82.2	16.0	2.7	1.27	3.82	1.78	0.75	0.37	2.16
2014	24	11.3	16.4	2587	26.2	77.1	85.9	16.8	3.3	1.56	4.55	2.12	0.89	0.44	2.57
2015	25	12.1	17.2	2213	25.6	77.9	86.8	16.9	0.8	0.37	1.74	0.81	0.34	0.17	0.98
Agali															
2011	32	14.9	17.3	1529	28.5	98.9	113.8	22.2	6.0	2.82	9.45	4.40	1.84	0.92	5.33
2012	33	15.5	17.9	1457	28.9	100.8	116.0	22.6	1.9	0.89	4.87	2.26	0.95	0.48	2.73
2013	34	15.8	18.6	1400	29.4	103.4	119.0	23.2	2.6	1.22	5.73	2.66	1.12	0.56	3.22
2014	35	16.2	19.2	1386	30.3	107.2	123.4	24.1	3.8	1.78	7.18	3.34	1.40	0.70	4.04
2015	36	17.2	20.0	1286	29.8	108.2	124.5	24.3	1.0	0.47	4.06	1.87	0.79	0.40	2.27
Kolleste 2															
2011	38	15.2	18.0	2733	49.5	167.5	190.5	37.1	6.4	3.00	8.61	4.02	1.68	0.84	4.86
2012	39	15.4	18.8	2733	50.8	173.3	197.1	38.4	5.8	2.71	7.97	3.72	1.55	0.78	4.50
2013	40	16.1	20.1	2467	50.4	174.9	198.9	38.8	1.6	0.75	3.24	1.50	0.63	0.32	1.82
2014	41	16.7	21.5	2300	50.3	176.8	201.1	39.2	1.9	0.89	3.59	1.67	0.70	0.35	2.02
2015	42	17.0	21.9	2300	52.4	181.3	206.2	40.2	4.5	2.11	6.57	3.06	1.28	0.64	3.70

Table 5
Annual aboveground litter C input (t C ha^{-1}) into soil in grey alder stands of different ages.

Year	Stand	Leaves	Branches	Other	Total
		(t C ha^{-1})			
2012	Kolleste 1	0.87	0.01	0	0.88
	Ilmatsalu	1.00	0.08	0.05	1.13
	Voopste	1.72	0.17	0	1.89
	Agali	1.73	0.18	0.08	1.99
	Kolleste 2	1.63	0.10	0.01	1.74
2013	Kolleste 1	1.02	0.01	0	1.03
	Ilmatsalu	1.66	0.04	0.26	1.96
	Voopste	1.77	0.09	0.02	1.88
	Agali	1.96	0.26	0.03	2.25
	Kolleste 2	1.86	0.14	0.05	2.05
2014	Kolleste 1	1.13	0.01	0	1.14
	Ilmatsalu	1.51	0.26	0.01	1.78
	Voopste	1.86	0.39	0.31	2.56
	Agali	1.70	0.27	0.29	2.26
	Kolleste 2	n.e	n.e	n.e	n.e

n.e. – not estimated.

Table 6
The above- and belowground biomass of the understorey herbaceous plants (t ha^{-1}) (±standard error).

Stand	Aboveground			Belowground
	2012	2013	2014	2013
Kolleste 1	n.e	1.03 ± 0.10	n.e	0.35 ± 0.13
Ilmatsalu	n.e	0.67 ± 0.06	n.e	0.40 ± 0.16
Voopste	0.81 ± 0.08	1.14 ± 0.13	1.63 ± 0.18	0.47 ± 0.09
Agali	1.29 ± 0.16	0.96 ± 0.07	1.21 ± 0.16	0.42 ± 0.12
Kolleste 2	n.e	0.77 ± 0.08	n.e	0.35 ± 0.07

n.e. – not estimated.

Table 7
The fine root characteristics of the studied grey alder stands of different ages. FRB - fine root biomass, FRP – fine root annual production (± standard error), FRN – fine root necromass. The fine root characteristics are calculated on the basis of the data for 2013.

Stand	FRB (t ha^{-1})	FRP (t ha^{-1})		FRN (t ha^{-1})	Turnover (year^{-1})	Longevity (year)
		2013	2014			
Kolleste 1	1.10 ± 0.17	1.46 ± 0.36	0.72 ± 0.29	0.61	1.33	0.8
Ilmatsalu	1.43 ± 0.12	1.79 ± 0.32	1.18 ± 0.17	0.58	1.25	0.8
Voopste	2.34 ± 0.28	1.78 ± 0.34	2.35 ± 0.46	0.60	0.76	1.3
Agali	1.36 ± 0.13	0.82 ± 0.10	0.86 ± 0.18	0.58	0.60	1.7
Kolleste 2	2.58 ± 0.17	1.74 ± 0.23	1.29 ± 0.21	0.56	0.67	1.5

3.5. Leaching of organic carbon

In 2013, the annual leaching of total organic carbon (TOC) in the Agali and in Voopste stands was low (26 and 19 kg ha^{-1} yr^{-1}, respectively). In the following year, leaching was significantly lower (9 kg ha^{-1} yr^{-1}) in the Agali stand. At the same time, in the younger Voopste stand it remained approximately at the same level during both study years. The major share of TOC leached in spring after the melting of snow (Fig. 3). Based on the data from Voopste and Agali, we assumed that the flux of TOC was negligible also in the other studied stands.

3.6. Soil respiration and the microclimate

The seasonal dynamics of soil respiration (Rs) (Fig. 4) and heterotrophic respiration (Rh) in all stands showed a similar pattern following changes in Ts. However, the seasonal dynamics of soil temperature (Ts) was similar in all stands (ranging from 4 to 18 °C) with a maximum in July. Among the stands, the highest mean Ts was recorded in Agali ($P < 0.05$, Appendix B). The efflux of CO_2 varied significantly between the stands (Table 8). In 2013, Rs and Rh were significantly lower in the Ilmatsalu and Agali stands than in the other studied three stands ($P < 0.05$). In 2014, Rs was significantly lower in Kolleste 1 and Agali than in Voopste; Rh was significantly lower in the Agali stand compared with the other two stands ($P < 0.05$). Trenching treatment did not affect Ts ($P > 0.05$) but increased soil moisture on average by 20% across the stands and over the measurement period ($P < 0.05$). Soil

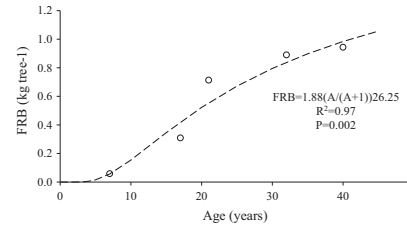


Fig. 2. Fine root biomass (FRB) per tree (kg) in the grey alder stands of different ages.

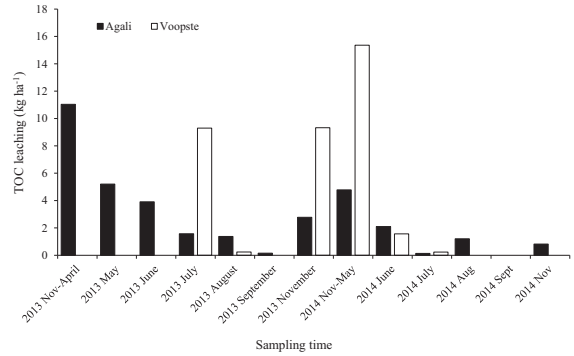


Fig. 3. The leaching dynamics of total organic carbon (TOC) in the Agali and Voopste grey alder stands.

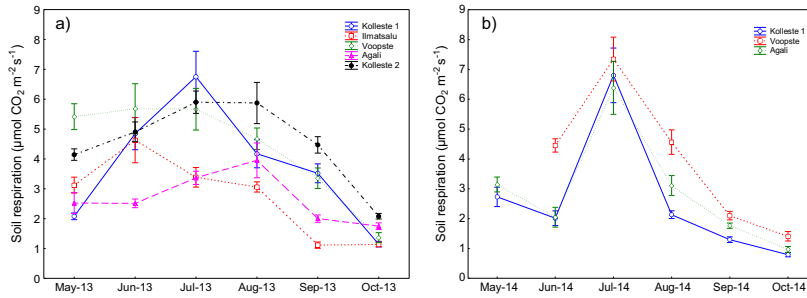


Fig. 4. Seasonal dynamics of soil respiration (Rs, µmol CO_2 m^{-2} s^{-1}) in differently aged grey alder stands in the growing season (May-October) of 2013 (a) and 2014 (b). Error bars represent standard error of the means.

Table 8
Annual soil (Rs) and heterotrophic (Rh) respiration, t C ha^{-1} yr^{-1} and average Rh/Rs ratio in 2013 and 2014.

Year	Stand	Rs	Rh	Rh/Rs ratio[a]
2013	Kolleste 1	7.8	5.6	0.71
	Ilmatsalu	5.8	2.7	0.46
	Voopste	9.9	4.9	0.50
	Agali	5.3	2.6	0.49
	Kolleste 2	9.9	5.8	0.59
2014	Kolleste 1	6.6	4.5	0.69
	Voopste	8.9	4.7	0.53
	Agali	6.5	2.9	0.45

[a] The Rh/Rs ratio is calculated for the period from May to November.

moisture fluctuated markedly throughout the growing season ranging from 11% to 69% in the studied stands. Among the stands, mean soil moisture content was the highest in Agali and Kolleste 1; soil was the driest in Kolleste 2 ($P < 0.05$, Appendix B).

Over 2013 and 2014, modelled annual Rs ranged from 5.3 to 9.9 t C ha^{-1} yr^{-1} and annual Rh ranged from 2.6 to 5.8 t C ha^{-1} yr^{-1}. The relative contribution of Rh to Rs for the period from May to November varied irrespective of stand age, showing the highest contribution of Rh to Rs in the youngest stand (Table 8).

The Ts was the main driver of seasonal variation in the soil CO_2 efflux. The Ts described 80–95% of variation in Rs; only in the youngest stand did Ts describe 67% of Rs in 2013 (Fig. 5). The same applied to Rh: in 2014, Ts described 88–94% of the variation in Rh; in 2013 the descriptive force of Ts was somewhat lower, at 53–81%.

The relationship between soil respiration and soil moisture differed between the stands. In most cases when soil moisture had a significant effect on the soil CO_2 effluxes this effect was negative. Only in the youngest stand did soil moisture exert a significant effect on Rs in both years (partial correlation, $R = -0.63$, $P = 0.036$). In the other stands, the effect of soil moisture on respiration rate was nonsignificant, or was expressed in only one year (regression analysis and partial correlation).

3.7. Carbon budgeting

Generally, the studied grey alder stands acted as C sequestration ecosystems, i.e. NEP was positive in most cases, ranging from −1.98 to +4.1 t C ha^{-1} yr^{-1}. The main C emission source was Rh,

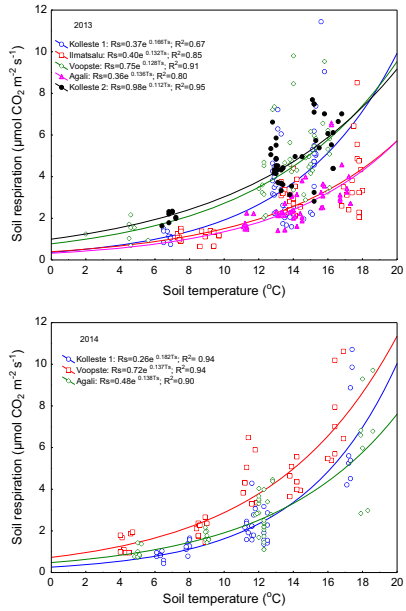


Fig. 5. Relationships between soil respiration (Rs) and soil temperature at a depth 5 cm of in Kolleste 1, Ilmatsalu, Voopste, Agali and Kolleste 2 in 2013 and in Kolleste 1, Voopste and Agali in 2014. An exponential Eq. (2) and determination coefficients for each stand are presented. $P < 0.001$ in all cases.

the share of C leaching from the ecosystem was negligible. The youngest stand was an exceptionally efficient C emitting system (Table 9) due to low NPP and intensive Rh in that year. However, in the following year the NPP was almost doubled and Rh was decreased which resulted as C sink into stand (1 t C ha^{-1} yr^{-1}) (Table 9). The NEP in the old Agali stand (34–35 years) was higher than in the younger stands (19–24 years), which can be attributed to high NPP and low Rh. The oldest grey alder stand was a modest C source, emitting 0.8 t C ha^{-1} yr^{-1}.

4. Discussion

4.1. Biomass production and carbon accumulation of trees

Repeated measurements, applied for stands of different ages, demonstrated a significant effect of the year, i.e. weather conditions, on the biomass production of the stands and hence on annual C accumulation in them (Tables 4 and 9). The biomass production of all studied stands was lower in 2013 (Table 4), which can be explained by droughty conditions. The vegetation period of 2013 was low in precipitation, from May to July it ranged from 164 mm to 124 mm according to the closest meteorological stations of Tõravere and Võru (Appendix A). Our earlier studies have confirmed that very dry summers may drastically decrease the CAP of grey alder stands (Uri et al., 2009; Aosaar et al., 2013); water limitation suppresses both the above- and belowground biomass production of young grey alder plants (Rytter, 2013). In the following year (2014), which was rainy, the CAP of all stands was one of the highest over the study period (Table 4): the amount of precipitation from May to July ranged from 302 mm to 234 mm according to the Tõravere and Võru stations, (Appendix A). Thus the drought stress in 2013 was removed already in the following year, which indicates the high adaptability and viability of grey alder.

Both stem mass and production in the oldest stand (Kolleste 2) was unexpectedly high (Fig. 1) compared to the average growing stock presented in the Estonian grey alder yield table (Uri et al., 2014). This was mainly due to higher stand density; the number of trees was almost twice as high as the average value for grey alder stands of the same age (Uri et al., 2014) owing to dense tree groups within the stand. High stand density also can be explained by the fact that almost all grey alder stands in Estonia are unmanaged. Standing biomass may be significantly lower in thinned stands than in unthinned stands, however, the biomass produced over the rotation period may be similar in both cases (Rytter, 1995). Average stem volume (0.16 m^3) exceeded the maximum

Table 9
The carbon budgets of the grey alder stands of different ages.

	Flux (t C ha^{-1} yr^{-1})	Kolleste 1 Stand age (years)		Ilmatsalu	Voopste		Agali		Kolleste 2
		9	10	19	23	24	34	35	40
	Plants aboveground								
1	Leafless tree biomass increment	1.02	2.30	1.48	1.78	2.12	2.66	3.34	1.50
2	Leaf litter	1.02	1.13	1.66	1.77	1.86	1.96	1.7	1.86
3	Branches + other litter	0.01	0.00	0.04	0.09	0.70	0.26	0.56	0.14
4	Herbaceous understorey production	0.44	0.46	0.29	0.49	0.70	0.41	0.61	0.33
Plants belowground									
5	Coarse root biomass increment	0.26	0.58	0.31	0.37	0.44	0.56	0.70	0.32
6	Tree fine root production	0.73	0.81	0.90	0.59	1.17	0.41	0.43	0.87
7	Understorey root and rhizome production	0.15	0.15	0.17	0.20	0.36	0.18	0.26	0.15
Output									
8	Heterotrophic respiration (C output)	5.6	4.5	2.7	4.9	4.7	2.6	2.9	5.8
9	TOC leaching	n.e	n.e	n.e	0.02	0.02	0.03	0.01	n.e
Soil									
10	C input = (2) + (3) + (4) + (6) + (7)	2.35	2.55	3.06	3.14	4.79	3.22	3.56	3.35
11	Soil C exchange = (10) − (8)	−3.25	−1.95	0.36	−1.76	0.09	0.62	0.66	−2.45
Productivity									
12	NPP = (1) + (2) + (4) + (5) + (6) + (7)	3.62	5.43	4.81	5.20	6.65	6.18	7.04	5.03
13	NEP = (12) − (8 + 9)	−1.98	0.93	2.11	0.30	1.95	3.58	4.14	−0.77

density line on the size-density diagram (Hibbs, 1987). Although this diagram has been compiled for red alder, it is probably useful for grey alder as well (Rytter, 1995). Kolleste 2 stand is an outlier in terms of the self–thinning rule which describes the competition-regulated relationship between tree size and stand density (Hibbs, 1987). However, some grey alder yield tables (Børset and Langhammer, 1966) report values for older stands, which are close to our results (Aosaar et al., 2012). High diversity of natural grey alder stands is a common feature that explains why forest growth models, among them yield tables, are always broad generalizations. As the abiotic and biotic factors of stands of different ages (soil properties, water regime, stand density, stand management, etc.) are always more or less varied, stand development cannot be completely simulated for similar sites (Uri et al., 2012). Yet the growth dynamics of the other four stands fits well the corresponding values of the Estonian grey alder growth model (Fig. 1, Table 3).

4.2. Aboveground litter and herbaceous understorey vegetation

The annual leaf litter flux was of the same magnitude across the stands, except for the youngest one where the amount of litter was approximately twice as low as that in the other stands. The average annual litter fall across all studied stands over the three study years was 3.5 t ha^{-1} yr^{-1}, which is higher than the mean annual total litter flux reported in extensive Finnish study: 2.3 t ha^{-1} yr^{-1} for both grey alder and black alder stands (Raulo and Hokkanen, 1989). In deciduous stands, both foliage mass and leaf area increase substantially during the early developmental stage, reaching optimal level and stabilizing thereafter. In the case of grey alder, this is consistent with relevant literature data (Rytter et al., 1989; Rytter and Rytter, 2016), as well with our earlier results (Uri et al., 2002, 2009), according to which the leaf mass of grey alder stands levels out at the age of 5–10 years. Annual leaf mass production may fluctuate depending on weather conditions during the growth period; there was found a negative impact of drought on foliage mass (Uri et al., 2009; Aosaar et al., 2016). Also liming treatment may considerably increase the production of leaf litter in *Alnus incana* stands (Huss-Danell, 1986).

The biomass production of the herbaceous understorey, accounting for 10–16% of the annual NPP of the stands, was not related to stand age and the C input from herbaceous aboveground biomass was relatively modest (Table 9). The share of the aboveground biomass of herbaceous plants exceeded the share of belowground biomass, which is contrary to results from silver birch stands (Varik et al., 2015) where the belowground biomass of herbaceous plants exceeded significantly their aboveground biomass.

4.3. Fine roots

Belowground biomass, particularly the fine roots, are essential for their contribution to C cycling in forest ecosystems (Brunner and Godbold, 2007). Relevant estimates of the biomass, production and turnover of the fine roots are definitely needed for compiling C models of forests. The FRB in the studied stands ranged from 1.1 t ha^{-1} to 2.6 t ha^{-1}, being the smallest in the youngest stand (Table 7), whose value is close to an earlier result for a 10-year-old grey alder stand (0.87 t ha^{-1}) (Aosaar et al., 2013). It is in good accordance with a Latvian study where the average FRB in mineral soils of young grey alder stands (4–9 years) was estimated at 1.2 ± 0.4 t ha^{-1} (Bardulis et al., 2015).

Fine root production (FRP) may vary a great deal depending predominately on the tree species, soil condition and stand age (Nadelhoffer and Raich, 1992; Eissenstat and Yanai, 1997). Regarding the FRP of grey alder, only a few results are available (Uri et al., 2011; Aosaar et al., 2013; Rytter, 2013). Estimation of FRP is complicated and labour consuming (Helmisaari et al., 2002; Xiao et al., 2008; Rytter, 2013). For this, several direct methods are used; in the present study we used the root mesh method (Hirano et al., 2009; Lukac and Godbold, 2010). However, it should be born in mind that each method has its advantages and disadvantages, which influence the result; thus selecting an appropriate method for estimation of FRP is always a challenge. The material of root mesh and the size of mesh aperture may affect the growth of fine roots through the mesh (Ohashi et al., 2015), depending mainly on the apical diameter of fine root tips (Montagnoli et al., 2014). We used a root mesh with an aperture size of 1.5 mm. As the mean diameter of fine alder roots is <0.65 mm across chronosequence stands (Jagodzinski et al., 2016), we assumed that the amount of fine roots that grew through the net reflects annual FRP. This assumption is supported by similar estimated FRP for two consecutive years (Table 7).

We assumed that the annual C input through fine root litter was equal with the fine root annual production. However, in our study the annual C input into soil via fine root litter may be underestimated since we sampled root meshes once per year, in October. According to Rytter (2013), quite a large part of short-living finest roots (<1 mm) may have very high turnover rate (5–6 yr^{-1}). We estimated our possible underestimation of FRP at 15–40% according to the data for a 17-year-old grey alder stand presented in Aosaar et al. (2013), while Rytter (2013) estimated fine root turnover for 3-year-old seedlings in a lysimeter experiment. Thus the estimated FRP in the studied stands is most probably an underestimation and the actual C input into soil via root litter may be even larger.

4.4. Carbon output

In the present study, both estimated annual fluxes i.e. total soil respiration (Rs) and heterotrophic soil respiration (Rh), varied across the grey alder stands of different ages and showed no clear trend in relation to stand age (Table 8). The Rh contributed the most to Rs in the youngest stand (Table 8) where annual C emission in 2013 was comparable to that of the oldest stand (5.6 versus 5.8 t C ha^{-1} yr^{-1}). It should be noted that the youngest stand is a naturally generated stand growing in a previous clear-cut area and the harvesting residues (dying root systems, stumps and other organic decomposing material) contributed greatly to Rh. Moreover, also the soil microclimate there (1.7 °C higher mean Ts of the growing season in 2013 than in 2014, and generally high moisture level) favoured the decomposition of organic matter. Soil temperature and moisture are known to be the main climatic factors associated with the soil CO_2 efflux (Hibbard et al., 2005; Luo and Zhou, 2006; Bahn et al., 2010; Gaumont-Guay et al., 2014). Contrary to our expectations, soil respiration was significantly lower in two stands – the middle-aged (Ilmatsalu) stand and the mature (Agali) stand. Low C:N ratio and strong correlation with soil temperature should lead to higher soil respiration. However, there are also other factors affect respiration. For example, respiration has been found to be related to FRB or FRP (Lee and Jose, 2003; Saiz et al., 2006; Knohl et al., 2008; Tang et al., 2009; Kukumägi et al., 2016). In the Agali stand, both FRB and FRP were significantly lower compared with the other stand (Table 7). However, after relating the annual soil respiration flux to stand density, these differences in soil respiration between the Ilmatsalu and Agali stands disappeared.

In the present study, the estimated annual C leaching from the Agali and Voopste stands was small and leached C made up only a minor proportion of the total C budget. Although C leaching was not directly measured for the three other stands, this did not affect the compiling of C budgets since TOC leaching was negligible.

4.5. Carbon budgeting

Several studies report that the magnitude of a forest C sink or C source varies with stand age (Law et al., 2003; Kolari et al., 2004; Pregitzer and Euskirchen, 2004). According to our earlier study of grey alder (Uri et al., 2014), C accumulation in the grey alder forest ecosystem is more intensive in younger and middle-aged stands, which is due to the dynamics pattern of biomass production.

Annual NEP in the studied stands fluctuated significantly during the 5-year study period and annual NEP depended on weather conditions in the current year rather than on stand age (Table 9). The effect of weather, especially precipitation and drought, may be revealed when one follows the annual biomass increment of grey alders (Uri et al., 2009; Aosaar et al., 2013).

According to literature data, mature stands can become weak C sinks or even sources of C (Goulden et al., 1996; Lindroth et al., 1998) since their annual biomass production decreases. On the other hand, soil Rh is another factor that plays an essential role here and stand age is reported to be one factor affecting soil respiration. However, different authors have reported an increase (Wiseman and Seiler, 2004), or a decrease (Saiz et al., 2006), in soil respiration, but also non-linear responses of soil respiration to stand age (Wang et al., 2002; Tang et al., 2009; Varik et al., 2015). The high NEP in the mature (Agali) stand can be attributed to high production, on the one hand, and to the low Rh fluxes, on the other. Also, the oldest stand, Kolleste 2, showed still vigorous growth but the high Rh flux changed this forest to a C emitting ecosystem. In unmanaged stands competition between trees and self-thinning may increase stand respiration and change the C balance towards the stand being a C source. However, all stands demonstrated considerable fluctuation in NPP during the 5-year study period (Table 4).

The effect of the year on the C budget was particularly pronounced in the youngest (Kolleste 1) stand where the leafless CAP for the two sequential years differed more than two times, turning the stand from a C source (-2 t C ha^{-1} yr^{-1}) into a C sink in the second year (+1 t C ha^{-1} yr^{-1}). Since Kolleste 1 was of sprout origin, then the share of the belowground fraction may have been higher and hence also annual NEP may be slightly underestimated. Yet soil C exchange was negative in both years in this forest (Table 9), which can evidently be attributed to its land use history: Kolleste 1 is a naturally regenerated stand growing on a previous clear-cut area with progressive decay of organic matter (roots, stumps, harvesting residues), which in turn contributes to soil Rh. As our earlier studies have shown (Uri et al., 2011, 2014; Aosaar et al., 2013), land use history is crucial in terms of capturing C by soil. The soil C storage increased when the annual organic C input into the soil exceeded the C output (Rh); such a situation occurred in the first generation alder stands (Uri et al., 2011, 2014; Aosaar et al., 2013). In the present study, the Agali stand was considered a first generation alder forest growing on previous agricultural land. Soil C exchange was highly positive, i.e. annual C capture by the soil was 0.65 t C ha^{-1} yr^{-1}. It is slightly lower than our earlier estimates (0.84–1.2 t C ha^{-1} yr^{-1}) (Aosaar et al., 2013; Uri et al., 2014) but fits well the range of the model-base estimation (0.34–0.68 t C ha^{-1} yr^{-1}) reported by Rytter and Rytter (2016). In a planted grey alder stand growing on previous agricultural land, total C sequestration in the upper 0–10 cm soil layer was 0.34 t C ha^{-1} yr^{-1} during 14 years (Uri et al., 2011). Negative soil C exchange is probably a temporary phenomenon for alder stands growing on a mineral soil. The C emission presumes presence of a large organic C pool in soil, which is a typical situation after stand harvesting. In the youngest stand the soil C storage was the largest (178 t C ha^{-1} yr^{-1}) (Table 2) among the five studied stands. Furthermore, it exceeded the average soil C storage of Estonian grey alder stands belonging to the same age class (5–10-years) (Uri et al., 2014). Intensive Rh in the oldest (Kolleste 2) stand is difficult to explain since the soil C pool is the lowest there (82.5 t C ha^{-1} yr^{-1}). Without doubt, soil type, fertility, water regime, etc. are also crucial factors affecting the soil C pool as well as the C sequester (Paul et al., 2003). However, the C budget for grey alder stands of different ages was positive in most cases, i.e. these stands were acting as C sinks.

The annual organic C input flux into soil (in the form of aboveground and belowground litter) was of similar magnitude in the studied stands, being between 3 and 3.5 t C ha^{-1} yr^{-1}, except for the youngest stand where it was lower (2.4 t C ha^{-1} yr^{-1}). The major share of aboveground litter was formed of leaf litter, which depended directly on foliage mass. The C flux from leaf litter and annual FRP accounted for 30–54% of the annual NPP of the stands and showed no correlation with stand age. However, the estimated FRP in the studied stands may be underestimated and the actual C input into soil via root litter can even be larger. The share of fine root litter or leaf litter in the total annual litter flux was also variable and did not depend on stand age.

Besides biomass production, also soil respiration intensity is a key factor affecting the stand C economy pattern. Still, the Rh flux for the two consecutive years was largely stable and varied less than annual NPP. It seems that compared with Rh, annual NPP is more sensitive to the weather conditions of a particular year. In the middle-aged Voopste stand, NEP was +0.3 t C ha^{-1} yr^{-1} in 2013 and +1.95 t C ha^{-1} yr^{-1} in 2014 while the annual Rh flux remained practically at the same level.

5. Conclusions

We hypothesized that grey alder stands growing at fertile sites act as carbon sinks at the young and middle-age stages while mature stands become C sources because of declined NPP. This hypothesis was proved partly; the oldest grey alder stand was indeed a weak C source. However, also young stands growing in post clear-cut areas may emit C at an earlier stage of development. This is due to decomposed organic matter from the previous forest generation, i.e. previous land use plays a crucial role in this respect. Generally, grey alder stands are C accumulating ecosystems, although the annual production of stands may be highly variable: the NPP of the same grey alder stands varied two to three times over the 5-year study period. Both annual NPP and NEP depended on the effect of a particular year, i.e. on weather conditions during the growing period rather than on stand age. Thus, owing to the high diversity of natural grey alder stands, growth modelling or C budgeting at the ecosystem's level are always broad generalizations. The repeated time-series measurement method yields more reliable estimation of C accumulation in forest ecosystems. However, use of this approach is very laborious and costly, which restricts its extensive application.

The results of the present study support our earlier finding that soil C exchange may depend on land use history; intensive C accumulation in soil took place in a stand growing on former agricultural land.

Grey alder stands on forest land accumulated C mainly in biomass, while in first generation stands (growing on previously non-forested land) C was transported both into soil and biomass.

Acknowledgements

This study was supported by the Estonian Science Foundation Grant No. 9342 and by the Institutional Research Funding IUT21-04 and IUT34-9 of the Estonian Ministry of Education and Research, as well as by the projects of Environmental Investment Centre Nos. 11-10-8/196 and 3406.

We thank Mrs. Ester Jaigma for revising the English text of the manuscript.

Appendix A. Precipitation according to the Tõravere and Võru meteorological stations during 2011–2015 (mm)

Year	April	May	June	July	August	Year total
	(mm month^{-1})					(mm)
Tõravere station						
2011	10.5	46.9	38.2	58.6	60.5	511.3
2012	39.7	76.3	88.6	69.3	103.3	771.5
2013	35.8	73.2	35.0	59.2	78.7	540.7
2014	16.2	90.1	133.5	78.0	126.2	701.1
2015	79.8	60.5	65.9	68.4	47.4	621.5
Võru station						
2011	12.0	85.6	36.8	83.4	78.4	575.8
2012	45.0	62.9	99.1	93.6	84.7	800.8
2013	40.8	39.5	25.0	59.5	56.1	532.1
2014	16.4	78.6	108.0	46.8	84.7	585.0
2015	71.4	58.1	36.1	106.7	41.2	608.5

Appendix B. Temperature (Ts, °C) and soil moisture (SWC, %) at 5 cm depth in control and trenched plots in Kolleste 1, Ilmatsalu, Voopste, Agali and Kolleste 2 in 2013 and in Kolleste 1, Voopste and Agali in 2014. Data represent mean ± SE of the growing season (May–October)

Year	Stand	Soil temperature		Soil moisture	
		Control	Trenched	Control	Trenched
2013	Kolleste 1	12.9 ± 0.41	12.8 ± 0.40	38.0 ± 2.52	47.8 ± 2.10
	Ilmatsalu	13.2 ± 0.56	13.1 ± 0.56	34.3 ± 1.90	47.4 ± 0.99
	Voopste	12.6 ± 0.57	12.7 ± 0.49	29.5 ± 1.71	34.5 ± 1.38
	Agali	14.3 ± 0.27	14.2 ± 0.29	39.0 ± 3.05	55.3 ± 3.06
2014	Kolleste 2	13.0 ± 0.42	12.9 ± 0.42	18.4 ± 1.24	24.4 ± 0.76
	Kolleste 1	11.2 ± 0.51	10.8 ± 0.61	39.3 ± 1.46	47.2 ± 1.45
	Voopste	11.0 ± 0.68	10.9 ± 0.66	29.4 ± 1.23	31.9 ± 1.17
	Agali	11.5 ± 0.58	11.1 ± 0.67	40.0 ± 1.80	47.5 ± 1.38

References

Ågren, G.I., Hyvönen, R., 2003. Changes in carbon stores in Swedish forest soils due to increased biomass harvest and increased temperatures analysed with a semi-empirical model. For. Ecol. Manage. 174, 25–37.

Aosaar, J., Varik, M., Uri, V., 2012. Biomass production potential of grey alder (*Alnus incana* (L.) Moench.) in Scandinavia and Eastern Europe: a review. Biomass Bioenergy 45, 11–26.

Aosaar, J., Varik, M., Lõhmus, K., Ostonen, I., Becker, H., Uri, V., 2013. Long-term study of above- and belowgroun, d biomass production in relation to nitrogen and carbon accumulation dynamics in a grey alder (Alnus incana (L.) Moench) plantation on former agricultural land. Eur. J. For. Res. 132 (5–6), 737–749.

Aosaar, J., Mander, Ü., Varik, M., Becker, H., Morozov, G., Maddison, M., et al., 2016. Biomass production and nitrogen balance of naturally afforested silver birch (*Betula pendula* Roth.) stand in Estonia. Silva Fenn. 50 (4), 1–19.

Bahn, M., Reichstein, M., Davidson, E.A., Grünzweig, J., Jung, M., Carbone, M.S., et al., 2010. Soil respiration at mean annual temperature predicts annual total across vegetation types and biomes. Biogeosciences 7, 2147–2157.

Bardulis, A., Lazdina, D., Daugaviete, M., Bardule, A., Daugavietis, U., Rozitis, G., 2015. Above ground and below ground biomass in grey alder *Alnus incana* (L.) Moench. young stands on agricultural land in central part of Latvia. Agron. Res. 13 (2), 277–286.

Benson, D.R., 1982. Isolation of *Frankia* strains from alder actinorhizal root-nodules. Appl. Environ. Microbiol. 44, 461–465.

Binkley, D., 2005. How nitrogen fixing trees change soil carbon. In: Binkley, D., Menyailo, O. (Eds.), Tree Species Effects on Soils: Implications for Global Change. NATO Sciences Series, Kluwer Academic Publishers, Dordrecht.

Børset, O., Langhammer, A., 1966. Vekst og produksjon i bestand av gråor (Alnus incana). [Growth and yield in stands of grey alder (Alnus incana)]. Scient. Rep. Agric. College Norway 45 (24), 1–34.

Brunner, I., Godbold, D.L., 2007. Tree roots in a changing world. J. For. Res. – Jpn. 12, 78–82.

Cannell, M.G.R., 1999. Growing trees to sequester carbon in the UK: answers to some common questions. Forestry 72 (3), 237–247.

Chapin, F.S., Woodwell, G.M., Randerson, J.T., Rastetter, E.B., Lovett, G.M., Baldocchi, D.D., et al., 2006. Reconciling carbon-cycle concepts, terminology, and methods. Ecosystems 9 (7), 1041–1050.

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J., 2001. Net primary production in forests: concepts and field methods. Ecol. Appl. 11 (2), 356–370.

Crawley, M.J., 2007. The R Book. John Wiley & Sons Ltd, p. 942.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. Science 263, 185–190.

Eissenstat, D.M., Yanai, R.D., 1997. The ecology of root life span. Adv. Ecol. Res. 27, 1–62.

Epron, D., 2009. Separating autotrophic and heterotrophic components of soil respiration: lessons learned from trenching and related root-exclusion experiments. In: Kutsch, W.L., Bahn, M., Heinemeyer, A. (Eds.), Soil Carbon Dynamics: An Integrated Methodology. Cambridge University Press, UK, pp. 157–168.

Fang, J.Y., Liu, G.H., Zhu, B., Wang, X.K., Liu, S.H., 2007. Carbon budgets of three temperate forest ecosystems in Dongling Mt. Beijing, China. Sci. China Ser. D: Earth Sci. 50, 92–101.

Gaumont-Guay, D., Black, T.A., Barr, A.G., Griffis, T.J., Jassal, R.S., Krishnan, P., et al., 2014. Eight years of forest-floor CO_2 exchange in a boreal black spruce forest: spatial integration and long-term temporal trends. Agric. For. Meteorol. 184, 25–35.

Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C., Wofsy, S.C., 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. Glob. Change Biol. 2, 159–168.

Granhall, U., Verwijst, T., 1994. Grey alder (*Alnus incana*) a N_2–fixing tree suitable for energy forestry. In: Hall, D.O., Grassi, G., Scheer, H. (Eds.), Biomass for Energy and Industry. Bochum, Germany, pp. 409–413.

Helmisaari, H.-S., Makkonen, K., Kellomäki, S., Valtonen, E., Mälkönen, E., 2002. Below- and aboveground biomass, production and nitrogen use in Scots pine stands in eastern Finland. For. Ecol. Manage. 165, 317–326.

Hibbard, K.A., Law, B.E., Reichstein, M., Sulzman, J., 2005. An analysis of soil respiration across northern hemisphere temperate ecosystems. Biogeochemistry 73, 29–70.

Hibbs, D.E., 1987. The self-thinning rule and red alder management. For. Ecol. Manage. 18, 273–281.

Hirano, Y., Noguchi, K., Ohashi, M., Hishi, T., Makita, N., Fujii, S., et al., 2009. A new method for placing and lifting root meshes for estimating fine root production in forest ecosystems. Plant. Root 3, 26–31.

Huss-Danell, K., 1986. Growth and production of leaf litter nitrogen by *Alnus incana* in response to liming and fertilization on degenerated forest soil. Can. J. For. Res. 16, 847–853.

Hytönen, J., Saarsalmi, A., 2009. Long-term biomass production and nutrient uptake of birch, alder and willow plantations on cut-away peatland. Biomass Bioenergy 33 (9), 1197–1211.

Hytönen, J., Saarsalmi, A., 2015. Biomass production of coppiced grey alder and the effect of fertilization. Silva Fenn. 49, 1. http://dx.doi.org/10.14214/sf.1260.

Jagodzinski, A.M., Ziółkowski, J., Warnkowska, A., Prais, H., 2016. Tree age effects on fine root biomass and morphology over chronosequences of *Fagus sylvatica*, *Quercus robur* and *Alnus glutinosa* stands. PLoS ONE 11 (2), e0148668. http://dx.doi.org/10.1371/journal.pone.0148668.

Knohl, A., Soe, A.R.B., Kutsch, W.L., Göckede, M., Buchmann, N., 2008. Representative estimates of soil and ecosystem respiration in an old beech forest. Plant. Soil 302, 189–202.

Kolari, P., Hari, P., Berninger, F., Pumpanen, J., Rannik, Ü., Ilvesniemi, H., 2004. Carbon balance of different aged Scots pine forests in Southern Finland. Glob. Change Biol. 10, 1106–1119.

Kukumägi, M., Ostonen, I., Uri, V., Helmisaari, H.-S., Kanal, A., Kull, O., Lõhmus, K., 2016. Variation of soil respiration and its components in hemiboreal Norway spruce stands of different ages. Plant. Soil. http://dx.doi.org/10.1007/s11104-016-3133-5.

Laiho, R., Sanchez, F., Tiarks, A., Dougherty, P.M., Trettin, C.C., 2003. Impacts of intensive forestry on early rotation trends in site carbon pools in the southeastern US. For. Ecol. Manage. 174, 177–189.

Law, B.E., Sun, O.J., Campbell, J., Van Tuyl, S., Thornton, P.E., 2003. Changes in carbon storage and fluxes in a chronosequnece of ponderosa pine. Glob. Change Biol. 9, 510–524.

Lee, K.-H., Jose, S., 2003. Soil respiration, fine root production, and microbial biomass in cottonwood and loblolly pine plantations along a nitrogen fertilization gradient. For. Ecol. Manage. 185, 263–273.

Lindroth, A., Grelle, A., Moren, A.S., 1998. Long-term measurements of boreal forest carbon exchange reveal large temperature sensitivity. Glob. Change Biol. 4, 443–450.

Lõhmus, E., 1984. Eesti Metsakasvukohatüübid. Tallinn, p. 76 (In Estonian).

Lõhmus, K., Mander, Ü., Tullus, H., Keedus, K., 1996. Productivity, buffering capacity and resources of grey alder forests in Estonia. In: Perttu, K., Koppel, A., (Eds.), Short Rotation Willow Coppice for Renewable Energy and Improved Environment. Uppsala, pp. 95–105.
Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. Bioscience 56, 395–405.
Lukac, M., Godbold, D.L., 2010. Fine root biomass and turnover in southern taiga estimated by root inclusion nets. Plant. Soil 331, 505–513.
Luo, Y., Zhou, X., 2006. Soil Respiration and the Environment. Elsevier Academic Press, UK.
McClaugherty, C.A., Aber, J.D., Melillo, J.M., 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 635, 1481–1490.
Meyer, A., Tarvainen, L., Nousratpour, A., Björk, R.G., Ernfors, M., Grelle, A., et al., 2013. A fertile peatland forest does not constitute a major greenhouse gas sink. Biogeosciences 10, 7739–7758.
Miežite, O., 2008. Structure and Productivity of Grey Alder Stands. Resume of the PhD paper. For the Scientific Degree of Dr. silv. in Forest Sciences. Jelgava, Latvia.
Montagnoli, A., Terzaghi, M., Scippa, G.S., Chiatante, D., 2014. Heterorhizy can lead to underestimation of fine-root production when using mesh-based techniques. Acta Oecol. 59, 84–90.
Mund, M., Kummetz, E., Hein, M., Bauer, G.A., Schulze, E.D., 2002. Growth and carbon stocks of a spruce forest chronosequence in central Europe. For. Ecol. Manage. 171, 275–296.
Nadelhoffer, K.J., Raich, J.W., 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology 73, 1139–1147.
Ohashi, M., Nakano, A., Hirano, Y., Noguchi, K., Ikeno, H., Fukae, F., et al., 2015. Applicability of the net sheet method for estimating fine root production in forest ecosystems. Trees 10, 1–8.
Paul, K.I., Polglase, P.J., Richards, G.P., 2003. Predicted change in soil carbon following afforestation or reforestation, and analysis of controlling factors by linking a C accounting model (CAMFor) to models of forest growth (3PG), litter decomposition (GENDEC) and soil C turnover (RothC). For. Ecol. Manage. 177, 485–501.
Peng, Y., Thomas, S.C., Dalung, T., 2008. Forest management and soil respiration: implications for carbon sequestration. Environ. Rev. 16, 93–111.
Pregitzer, K.S., Euskirchen, E.S., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Glob. Change Biol. 10, 2052–2077.
Pussinen, A., Karjalainen, T., Mäkipää, R., Valsta, L., Kellomäki, S., 2002. Forest carbon sequastration and harvest in Scots pine stand under different climate and nitrogen deposition scenarios. For. Ecol. Manage. 158, 103–115.
Raulo, J., Hokkanen, T., 1989. Harmaa-ja tervalepän karikesato. Summary: litter fall of Alnus incana and Alnus glutinosa. Folia For. 738, 25.
Rytter, L., 1989. Distribution of roots and root nodules and biomass allocation in young intensively managed grey alder stands on a peat bog. Plant. Soil 119, 71–79.
Rytter, L., Šlapokas, T., Granhall, U., 1989. Woody biomass and litter production of fertilized grey alder plantations on a low-humified peat bog. For. Ecol. Manage. 28, 161–176.
Rytter, L., 1995. Effects of thinning on the obtainable biomass, stand density, and tree diameters of intensively grown grey alder plantations. For. Ecol. Manage. 73, 135–143.
Rytter, L., 1996. Grey alder in forestry: a review. Norwegian J. Agric. Sci. 24, 65–84.
Rytter, R.-M., 2013. The effect of limited availability of N or water on C allocation to fine roots and annual fine root turnover in *Alnus incana* and *Salix viminalis*. Tree Physiol. 33, 924–939.
Rytter, L., Rytter, R.-M., 2016. Growth and carbon capture of grey alder (*Alnus incana* (L.) Moench.) under north European conditions – estimates based on reported research. For. Ecol. Manage. 373, 56–65.
Saarsalmi, A., 1995. Nutrition of Deciduous Tree Species Grown In Short Rotation Stands (Dissertation). University of Joensuu, Finland.
Saarsalmi, A., Palmgren, K., Levula, T., 1985. Leppäviljelmän biomassan tuotos sekä ravinteiden ja veden käyttö. Folia For. 628, 24 (In Finnish, with English summary).
Saiz, G., Bydrne, K.A., Butterbach-Bahl, K., Kiese, R., Blujdea, V., Farrell, E.P., 2006. Stand age-related effects on soil respiration in a first rotation Sitka spruce chronosequence in central Ireland. Glob. Change Biol. 12, 1007–1020.
Schmidt, M., Kiviste, A., Gadow, K.v., 2011. A spatially explicit height–diameter model for Scots pine. Eur. J. For. Res. 130 (2), 303–315.
Somogyi, Z., Bidlo, A., Csiha, I., Illes, G., 2013. Country-level carbon balance of forest soils: a country-specific model based on case studies in Hungary. Eur. J. For. Res. 132 (5–6), 825–840.
Soosaar, K., Mander, Ü., Maddison, M., Kanal, A., Kull, A., Lõhmus, K., et al., 2011. Dynamics of gaseous nitrogen and carbon fluxes in riparian alder forests. Ecol. Eng. 37, 40–53.
Tang, J., Bolstad, P.V., Martin, J.G., 2009. Soil carbon fluxes and stocks in a Great Lakes forest chronosequence. Glob. Change Biol. 15, 145–155.
Telenius, B.F., 1999. Stand growth of deciduous pioneer tree species on fertile agricultural land in southern Sweden. Biomass Bioenergy 16, 13–23.
Uri, V., Tullus, H., Lõhmus, K., 2002. Biomass production and nutrient accumulation in short-rotation grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural agricultural land. For. Ecol. Manage. 161 (1–3), 169–179.
Uri, V., Tullus, H., Lõhmus, K., 2003. Nutrient allocation, accumulation and aboveground biomass in grey alder and hybrid alder plantations. Silva Fenn. 37 (3), 301–311.
Uri, V., Lõhmus, K., Kiviste, A., Aosaar, J., 2009. The dynamics of biomass production in relation to foliar and root traits in a grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural land. Forestry 82 (1), 61–74.
Uri, V., Lõhmus, K., Mander, Ü., Ostonen, I., Aosaar, J., Maddison, M., et al., 2011. Long-term effects on the nitrogen budget of a short-rotation grey alder (*Alnus incana* (L.) Moench) forest on abandoned agricultural land. Ecol. Eng. 37, 920–930.
Uri, V., Varik, M., Aosaar, J., Kanal, A., Kukumägi, M., Lõhmus, K., 2012. Biomass production and carbon sequestration in a fertile silver birch forest chronosequence. For. Ecol. Manage 267, 117–126.
Uri, V., Aosaar, J., Varik, M., Becker, H., Ligi, K., Padari, A., et al., 2014. The dynamics of biomass production, carbon and nitrogen accumulation in grey alder (*Alnus incana* (L.) Moench) chronosequence stands in Estonia. For. Ecol. Manage. 327, 106–117.
Varik, M., Aosaar, J., Ostonen, I., Lõhmus, K., Uri, V., 2013. Carbon and nitrogen accumulation in belowground tree biomass in a chronosequence of silver birch stands. For. Ecol. Manage. 302, 62–70.
Varik, M., Kukumägi, M., Aosaar, J., Becker, H., Ostonen, I., Lõhmus, K., et al., 2015. Carbon budgets in fertile silver birch (*Betula pendula* Roth) chronosequence stands. Ecol. Eng. 77, 284–296.
Wang, C.K., Bond-Lamberty, B., Gower, S.T., 2002. Soil surface CO_2 flux in a boreal black spruce fire chronosequence. J. Geophys. Res. 107, 8224.
Waring, R.H., Running, S.W., 2007. Forest Ecosystems: Analysis at Multiple Scales. Academic Press, San Diego, pp. 263–291.
Wiseman, P.E., Seiler, J.R., 2004. Soil CO_2 efflux across four age classes of plantation loblolly pine (*Pinus taeda* L.) on the Virginia Piedmont. For. Ecol. Manage. 192, 297–311.
WRB, 2006. World Reference Base for Soil Resources 2006, second ed. World Soil Resources Reports No. 103. FAO, Rome.
Xiao, C.W., Sang, W.G., Wang, R.-Z., 2008. Fine root dynamics and turnover rate in an Asia white birch forest of Donglingshan mountain, China. For. Ecol. Manage. 255, 765–773.

IV

Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., **Morozov, G.**, Karoles, K. (2017). Ecosystems carbon budgets of differently aged downy birch stands growing on well-drained peatlands. Forest Ecology and Management, 399: 82−93.

Forest Ecology and Management 399 (2017) 82–93

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Ecosystems carbon budgets of differently aged downy birch stands growing on well-drained peatlands

Veiko Uri [a,*], Mai Kukumägi [b], Jürgen Aosaar [a], Mats Varik [a], Hardo Becker [a], Gunnar Morozov [a], Kalle Karoles [a]

[a] Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, 51014 Tartu, Estonia
[b] Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia

ARTICLE INFO

Article history:
Received 10 February 2017
Received in revised form 8 May 2017
Accepted 13 May 2017
Available online 23 May 2017

Keywords:
Betula pubescens
Drained peatland
Net ecosystem production
Soil respiration
Carbon fluxes
Aboveground and fine root litter

ABSTRACT

Estimation of the carbon (C) storages and fluxes in different forest ecosystems is essential for understanding their C sequestration ability. The net ecosystem production (NEP) and the net primary production (NPP) in five downy birch (*Betula pubescens*) stands, aged between 12 and 78 years, growing on fertile well-drained *Histosols*, were studied. Drainage of swamp forests is a large-scale manipulation, which causes significant shifts at the ecosystems level, altering C and nutrient cycling a great deal. Young and middle-aged downy birch stands (12–30-year-old) acted as C sink ecosystems, accumulating 1.4–3.0 t C ha^{-1} yr^{-1}. In the 38-year-old stand NEP was roughly zero; annual C budget was almost in balance. The over-matured downy birch stand (78-year-old) acted as a C source emitting 0.95 t C ha^{-1} yr^{-1}. Annual woody biomass increment of the stand was the main factor which affected the forest to act as a C accumulating system. Although the highest heterotrophic respiration (Rh) values were measured in the middle-aged stands, mean soil C emission did not differ significantly between the studied stands. Annual total soil respiration (Rs) and Rh ranged from 7.4 to 8.8 t C ha^{-1} and 4.7 to 6.2 t C ha^{-1}, respectively. Soil temperature appeared to be the dominant driver of the soil CO_2 effluxes. Temperature sensitivity (Q_{10} value) of respiration rates (3.0–5.5), as well as the Rh/Rs (0.6–0.7) varied irrespective of stand age. Both the annual aboveground litter (1.5–1.9 t C ha^{-1} yr^{-1}) and fine root litter (0.9–1.5 t C ha^{-1} yr^{-1}) input fluxes were quite similar for the studied stands. However, the annual organic C input into the soil via above- and belowground litter was smaller than the annual Rh efflux, indicating that continuous mineralization of the peat layer reduces the soil organic C pool. The main share of the C stock in the drained swamp downy birch stands was soil C; the storage of C accumulated in the woody biomass of the trees accounted for only 5–20% of the total C storage of the ecosystem.

1. Introduction

Carbon (C) accumulation in forest ecosystems is an actual topic in terms of climate change and intensive forest management (Schimel et al., 2001; Walle et al., 2007; Verlinden et al., 2013; Wu et al., 2013). Boreal and temperate forests play an important role in global C sequestration (Dixon et al., 1994; Peng et al., 2008) and have a great potential to sequester C in short- or mid-term. There are many factors which can affect the rate of C sequestration in forests: tree species, stand age, site fertility and even the impact of the understorey cannot be disregarded (Vogel and Gower, 1998). Also forest management is closely related to C sequestration, while drainage may significantly affect stands C cycling (Ojanen et al., 2010; Lohila et al., 2011; Meyer et al., 2013; Birdsey and Pan, 2015).

Estimation of the C storages and fluxes in different forest ecosystems is an important task for understanding their C sequestration ability. Forests in the boreal and hemiboreal zones usually act as C sinks (Liski et al., 2003; Kaipanen et al., 2004) and both forest biomass and soil are considered to have a large potential for the C storage (Gower, 2003; Houghton, 2005). However, there is still a large gap in empirical data about C cycling in various forest ecosystems. Due to the large heterogeneity of different forest ecosystems, their C cycling may be highly variable. A crucial issue is the quantification and modelling of the main output and input C fluxes in different forests and in the case of different management regimes. Also the ratio of C accumulated in the soil to C accumulated into the biomass of trees has been highlighted as it determines the period of C capture (Peltoniemi et al., 2004; Uri et al., 2012).

* Corresponding author.
E-mail address: veiko.uri@emu.ee (V. Uri).

http://dx.doi.org/10.1016/j.foreco.2017.05.023
0378-1127/

In northern latitudes, the amount of annual precipitation exceeds transpiration, creating favourable conditions for the paludification process and for accumulation of a significant share of the world's soil C pool in peatlands (Gorham, 1991; Martikainen et al., 1993). Thus these areas have the potential to significantly influence the global atmospheric budget of greenhouse gases (GHG) (Martikainen et al., 1993; von Arnold et al., 2005a; Leppelt et al., 2014). Draining of excessively moist soils in order to improve growth conditions for forests has been a common practice in northern regions, which has resulted in an increase of the productive forest land area. For instance, drained peatlands in Finland constitute 34% of the global area of forestry-drained peatlands (Lohila et al., 2011). In Estonia, 37% of the total forest area are located on organic soils and among them 15%, i.e. 328,000 ha, are classified under full-drained peatland forests (Yearbook Forests, 2013). As a result of the long term drainage of swamps, there has emerged a novel specific site type, named "*Oxalis* full-drained swamp", according to local classification (Lõhmus, 1984). Drainage is an extensive disturbance, which can cause significant shifts at the ecosystem's level and can affect C balance between photosynthesis and soil respiration (Goulden et al., 1996; Lindroth et al., 1998; Hyvönen et al., 2007). Since forest drainage in Estonia was very intensive in the second half of the 20th century, the total area of forests affected by drainage is up to 560,000 ha (Yearbook Forests, 2013). It is estimated that about 70% of all Estonian peatlands are more or less affected by drainage (Paal, 1998).

Assuming that CO_2 emission from forests growing on drained organic soils may be significantly increased due to the intensive mineralization of soil organic matter (SOM), these forests deserve special attention. Heterotrophic soil respiration (Rh), derived from decomposition of litter and SOM, is one of the largest C fluxes in ecosystems (Harmon et al., 2011) and is strongly favoured by drainage (Silvola et al., 1996). Does the ecosystem of drained forest act as a carbon sink or source, i.e. does more intensive C accumulation through increased biomass production exceed intensified Rh? This is a widely discussed issue, which is closely related to site fertility and management of drained peatland forests. Drained and nutrient rich afforested organic soils are potential sources of GHG, contributing to global warming (Leppelt et al., 2014); after drainage, some peatland ecosystems have turned from a C sink to a C source (Ilomets, 1996; Bonan, 2008).

Regarding downy birch, we did not find any earlier literature data about C budget despite the wide natural distribution area of this species on the Eurasian continent. The most abundant birch resources are located in temperate and boreal forests of Northern Europe where it is a commercially important birch species (Hynynen et al., 2010). Downy birch is also the most common tree species on lowland *Histosols* in Estonia.

The main objective of the present study was to analyse the dynamics of C cycling in downy birch stands of different ages, growing on long-term drained swamps, by applying the C budgeting approach.

To compile C budgets we aimed to estimate the above- and below-ground biomass and production, as well as soil respiration efflux in five downy birch stands.

2. Material and methods

2.1. Study sites

Five naturally regenerated pure downy birch stands, aged between 12 and 78 years, growing in fertile *Oxalis* full-drained swamp site type (Lõhmus, 1984) were included in the study (Table 1). Long lasting drainage of peatlands causes gradual changes in site properties; the productivity and composition of understorey species change similarly to a forest growing on mineral soils, making drained areas more favourable for tree growth as well as for forest management.

All studied stands are located in the Järvselja experimental forest district in the eastern part of Estonia. The area belongs to the hemiboreal vegetation zone (Ahti et al., 1968), which is a transition zone from the temperate to boreal climate. The Järvselja forest district is an area with a long drainage history (first drainage systems from the end of the 19th century) and drained forests are widespread in this region. The *Oxalis* full-drained swamp site type made up 14% of the forest district (Korjus et al., 2015). All studied sites were drained approximately 40–50 years earlier using open ditches. As a result of drainage, the groundwater level was normally below 40 cm from surface during the vegetation period. According to the closest meteorological station of Tõravere, the annual average precipitation is 680 mm, and annual average temperature is 5.8 °C. A sample plot with an area of 0.063 ha was established in each studied stand and the main stand characteristics were determined (Table 1).

All studied stands were of natural origin and unmanaged, i.e. unthinned before the establishment of the sample plots. As typical for *Oxalis* full-drained swamp forest, mainly herbaceous plants were growing in the understorey.

All studied stands grow on drained organic soils (*Histosols*) where high C and N content (20–30% and up to 3%, respectively) as well as a thick organic horizon (>40 cm) are inherent (WRB, 2006). In all studied stands, one soil pit (depth to 0.7 m) was dug for estimation of the soil type. For estimation of the thickness of the peat layer, additional sampling from the bottom of the soil pit was done using a soil probe.

Well decomposed peat soil was dominating at all study sites; the thickness of the peat layer varied between the sites (Table 2). Although all stands belonged to the same site type, the peat layer was thinner in older stands. The C:N ratio for peat was higher for the oldest stand, which is most probably caused by the soil properties before drainage.

For estimating soil C and nutrient content, samples from 20 random points at depths of 0–10; 10–20; 20–30; 30–40 and 40–50 cm soil layers were taken over the stand to form composite samples separately for each stand. Altogether five replicates for each layer were analysed for C, nutrients and pH (Table 2).

For calculating the C and N storages in the soil, soil bulk density was determined. In the soil pit, bulk density samples were taken from different soil layers (0–50 cm) with a stainless steel cylinder (d = 40 mm, V = 50 cm^3) avoiding compression of the soil and preserving soil structure. Three samples were taken from each depth layer. The bulk density samples were dried at the laboratory at 105 °C to constant weight and weighed. The soil analyses were carried out at the Biochemistry Laboratory of the Estonian University of Life Sciences.

2.2. Aboveground biomass and production of the stands

The aboveground woody biomass and production of the stands was estimated in September-October 2014 when the process of biomass formation was completed; the model tree method (Bormann and Gordon, 1984; Uri et al., 2007a,b, 2012, 2014) was used. For this, a sample plot was established in each stand. All trees growing in the sample plot were measured for breast height diameter ($D_{1.3}$) and additional 10–15 trees were measured for height to estimate average stand height. The trees were divided into five classes on the basis of $D_{1.3}$, and a model tree was selected randomly from each class. A total of 5–7 per model trees per stand were felled in the leafless stage and their biomass was estimated. The stems of the model trees from the youngest stand (12-year-

Table 1
Main characteristics of the downy birch (DB) stands; $D_{1.3}$ – average diameter at breast height, H – average height, BA – basal area, N – stand density. For $D_{1.3}$ and H, standard error is presented.

Stand	Location	Area of stand, ha	Age, yr	$D_{1.3}$, cm	H, m	BA, m^2 ha^{-1}	N, trees ha^{-1}
DB-12	N 58°15′ E 27°16′	4.2	12	7.9 ± 0.2	12.0 ± 0.6	13.5	2752
DB-24	N 58°15′ E 27°15′	2.1	24	11.5 ± 0.4	14.7 ± 1.9	19.6	1888
DB-30	N 58°18′ E 27°21′	5.1	30	13.7 ± 0.4	15.2 ± 0.9	24.5	1664
DB-38	N 58°17′ E 27°19′	2.7	38	11.9 ± 0.4	14.6 ± 1.4	18.8	1696
DB-78	N 58°17′ E 27°13′	1.6	78	17.9 ± 0.6	19.3 ± 0.4	19.4	768

Table 2
Soil characteristics of the studied stands. C – organic carbon, N – Kjeldahl nitrogen, P – available (AL) phosphorus, K – available (AL) potassium, Ca – available calcium and Mg – available magnesium. Presented average concentrations in the upper 30 cm soil layer.

Stand	Soil type	Depth of peat, cm	C	N	P	K	Ca	Mg	pH_{KCl}	C	N
			%		mg kg^{-1}					t ha^{-1}	
DB-12	*Eutric Haplic Histosol*	>100	43.0	2.94	77.8	196.6	4998.6	705.9	4.78	562[a]	34.7[a]
DB-24		>100	41.7	2.78	79.9	215.9	3524.0	611.0	3.75	658[a]	43.2[a]
DB-30		>100	41.6	2.68	29.4	141.0	7260.1	719.9	4.22	746[a]	52.2[a]
DB-38		70	35.9	2.94	30.6	151.8	5905.9	546.5	4.31	529	38.5
DB-78		45	24.6	1.23	16.3	62.1	2664.8	306.9	4.72	265	13.5

[a] Storage only for the upper 100 cm peat layer.

old) (Table 1) were divided into five sections: the first section 0–1.3 m, the second section 1.3 m up to the living crown; and the living crown was divided into three equal layers. For the older stands where the trees had larger dimensions, the stems were divided as follows: the first section 0–1.3 m; the subsequent sections 2 m, followed by the section up to the living crown; and the living crown was divided into three sections of equal length.

The stem sections and the branches of different crown sections were weighed in the forest and from every crown section, one average model branch was selected and taken to the laboratory. In the laboratory, the living branches were divided into twigs (i.e. current-year shoots) and older branches. From every fraction, a subsample was taken for estimation of dry matter content, as well as for chemical analysis. The samples of the fractions were dried at 70 °C until constant weight and weighed to 0.01 g. The share of the wood and bark of the stems was determined. The dry mass of the different fractions was calculated for each model tree by multiplying the corresponding fresh mass by the dry matter ratio (Uri et al., 2007a, 2007b, 2012).

For estimating the aboveground biomass of the stand, an allometric Eq. (1) provided the best fit:

$$y = a\, D_{1.3}^{b}, \quad (1)$$

where

y is the aboveground biomass or stemwood production of a model tree, (g),
$D_{1.3}$ is breast height diameter (cm),
a and b are parameters (Table 3).

For estimating the biomass of the different compartments (twigs, old branches and stems), we used the percentage distribution of the fractions obtained from the model trees, which is a highly stable parameter according to our earlier studies (Uri et al., 2007a, 2007b, 2009, 2012).

The current annual production (CAP) of the stemwood was estimated on the basis of the annual rings (Uri et al., 2012, 2014). Cross section disks were cut from the middle of each stem section, dried and polished, and the width of the annual rings was measured to 0.001 mm using the TSAP-Win (Copyright © 2003 Frank Rinn, Heidelberg, Rinn Tech) software.

Annual wood increment for the sections of the model trees was calculated according to Eq. (2) (Whittaker and Woodwell, 1968)

$$W_i = W_0(r^2 - (r - i)^2)/r^2 \quad (2)$$

where

W_i is the annual dry mass increment of wood (g),
W_0 is the dry mass of wood (g),
r is the radius of the analysed disk (mm),
i is the thickness of an annual ring (mm).

The production of the stem sections was summed up for calculation of the stem mass production of the tree. Allometric relationship (1) was used to estimate the annual production of stem mass on the basis of tree diameter (Table 3). The relative increments of the fractions of the stem wood and bark were assumed to be equal.

2.3. Stemwood density

Stemwood density was estimated by using the xylometric method (water displacement principle for volume estimation (Uri et al., 2014, 2015). Oven-dried test pieces were submerged in a container (10 L) with an overflow channel which was filled with

Table 3
Parameter estimates (a, b) of regression Eq. (1) for estimation of the aboveground woody biomass and current annual production (CAP) of the stem mass of downy birch (g). R^2-coefficient of determination; $P < 0.001$ in all cases.

Stand	Aboveground woody biomass			CAP of stem mass		
	a	b	R^2	a	b	R^2
DB-12	76.98	2.56	0.99	0.74	3.62	0.99
DB-24	84.51	2.46	0.95	0.33	3.48	0.91
DB-30	81.73	2.52	0.99	4.51	2.42	0.91
DB-38	71.88	2.61	0.96	1.88	2.73	0.97
DB-78	248.08	2.19	0.98	9.84	1.99	0.74

water. The volume of removed water was measured by weighing; every test piece was weighed before and after sinking as wood is a hygroscopic substance; for accurate estimation, the water bound in the wood of the test piece was taken into account. Stemwood test pieces were taken from every felled model tree in all sample plots of different stands. Samples were sawn from sections of different height and average stemwood density per tree was calculated as weighted average. To convert the stem mass values to the stem volume values, the corresponding density value for each stand was used.

2.4. Belowground biomass and production of stands

2.4.1. Stumps and coarse roots

Coarse root biomass (CRB) was estimated by excavating the root system of one average model tree in 30-year-old stand. The excavated root system was carefully washed and separated into the following fractions in the laboratory: d < 2 mm, 2 mm ≤ d < 5 mm, 5 mm ≤ d < 10 mm, d ≥ 10 mm and the stump core (Varik et al., 2013). From every fraction, a subsample was taken for estimation of dry matter content as well as for chemical analysis. The samples were dried at 70 °C until constant weight and weighed to 0.1 g. The root-shoot ratio was calculated as the percentage of coarse root biomass from aboveground woody leafless biomass. We excluded the fine root fraction (d < 2 mm) from this calculation because of considerable losses (65–75%) from this root fraction (Lõhmus et al., 1991; Uri et al., 2002).

Coarse root production (CRP) was calculated on the basis of the equal relative increments of aboveground woody biomass; the relative increments of the aboveground and belowground woody biomass fractions were assumed to be equal (Aosaar et al., 2013, 2016; Varik et al., 2015).

2.4.2. Fine roots

Fine root (d < 2 mm) biomass (FRB) was estimated with the soil coring method (Vogt et al., 1983; Varik et al., 2013). Twenty soil cores were taken randomly over the whole stand with a cylindrical corer with a diameter of 38 mm in October 2014. The soil cores were divided into four layers (0–10; 10–20; 20–30 and 30–40 cm), placed in polyethylene bags and transported to the laboratory and frozen (−18 °C) until analysis.

The roots were washed free of soil and separated under a microscope into tree roots and the roots of the herbaceous understorey vegetation. The samples were dried at 70 °C and weighed to 0.001 g. The FRB per hectare was calculated by summing up the average values of fine root mass for the successive soil layers from the soil cores. The FRB per tree was calculated by dividing fine root biomass per hectare by the stem number per hectare (Finér et al., 2007).

For calculating the annual C flux into the soil through root litter, the fine root production (FRP) was estimated by using the root mesh (root inclusion net) method (Hirano et al., 2009; Lukac and Godbold, 2010; Ohashi et al., 2016; Uri et al., 2017). Nylon meshes (25 × 7 cm) were placed vertically into the forest soil of all studied stands to a depth of 20 cm, according to a detailed description in Hirano et al. (2009), in the autumn of 2013. The first samples (25) were harvested 1 year after placement, i.e. in October 2014, using a spade. A soil block around the net (20 × 20 × 20 cm) was excavated and placed carefully into a plastic bag. The samples were preserved in a refrigerator until processing. To reach the nets and fine roots, the soil was carefully peeled off at 1 cm from both sides of the net with a long-bladed knife and scissors so that the roots penetrating the net were not removed. The formed soil block was carefully shaken free of soil, and the net with the roots was submerged in water. The fine roots of birch as well as the roots of herbaceous plants were washed out and carefully removed from the net. The separated fine roots of birch and herbaceous plants were dried at 70 °C and weighed.

Fine root turnover rate was calculated by dividing FRP ($g\,m^{-2}\,yr^{-1}$) by FRB ($g\,m^{-2}$) (McClaugherty et al., 1982). Fine root longevity (yr^{-1}) was calculated as the reciprocal of root turnover rate. Since the root mesh method enables to estimate FRP only for the upper 0–20 cm soil layer, we used extrapolated FRB for the deeper (20–40 cm) soil layer. By using FRP and average C concentration of fine roots, the annual C input to the soil was calculated.

2.5. Herbaceous understorey plants

For each study site, ten random samples (area 1 m^2 each) over the whole stand were taken in mid-July when the aboveground biomass of the herbaceous understorey vegetation was at a maximum. The aboveground part of all herbaceous plants was harvested from a 1 m^2 quadrate and weighed. Subsamples were taken for dry matter content and for chemical analysis. The samples were dried at 70 °C to constant weight and weighed to 0.01 g. The samples were analysed for C concentration**.** As the aboveground part of herbs is annual, their aboveground production is assumed to be equal to biomass.

The belowground biomass of the understorey was estimated on the basis of soil cores. Ten soil cores were taken to a depth of 30 cm in the same 1 m^2 quadrates using a soil auger (d = 4.8 mm). All cores were divided into three subsequent 10 cm layers and the roots and rhizomes were washed out of each layer. The roots and rhizomes of the herbaceous plants were separated from the birch roots under a microscope and were carefully cleaned of soil particles. The samples were dried at 70 °C to constant weight and weighed to 0.001 g. For the belowground fraction of the understorey, turnover rate was assumed to be 1 year (Lõhmus et al., 2002; Uri et al., 2011).

2.6. Aboveground litter flux

Seven litter traps (collecting area 0.36 m^2 each) were placed randomly into each stand in the summer 2013 and litter was sampled once a month (once a fortnight during leaf fall) until the end of 2015. For the present study, the data of 2014 were used. The collected samples were divided into different fractions: leaves, branches and other material (e.g. seeds, pieces of bark, buds etc.). The amount of C introduced to the soil via litter was calculated by multiplying the amount of litter by the corresponding C concentration.

2.7. Soil respiration and heterotrophic respiration measurements

Soil respiration rates were measured once a month from May to November 2014 using the method of the closed dynamic chamber (PP *Systems* SRC-1 chamber (volume 1170 cm^3, enclosed soil surface 78 cm^2) with a gas analyser CIRAS-2 (Differential CO_2/H_2O Infrared Gas Analyzers)). To distinguish heterotrophic respiration (Rh) from total soil respiration (Rs), the trenching method with insertion of 8 deep PVC cylinders (inner diameter 20 cm, height 60 cm) to a depth of 50 cm was applied in April 2014. Trenching to a depth of 50 cm can be considered sufficient as the main share of the fine root biomass of birch is located in the upper 0–20 cm soil layer (Uri et al., 2007a; Varik et al., 2013). The distance between the trenching cylinders was approximately 5–10 m. At approximately 50 cm from each deep PVC cylinder, collars (diameter 10 cm, height 5 cm) for Rs measurement (control) were installed at a depth ~2–3 cm. The herbaceous vegetation was carefully removed from the inside of the deep cylinder and the collar with minimum soil disturbance, and both were kept free of the live

vegetation throughout the study. Soil temperature (Ts, °C) was measured simultaneously with soil respiration in the control and trenched plots using an attached soil temperature probe STP-1 (PP Systems International, Inc., USA) inserted at a depth of ~5 cm. Volumetric soil moisture (%) was also measured at a depth of ~5 cm using a HH2 Moisture Meter Version 2 (Delta-T Devices Ltd, UK). In addition, soil temperature (model 1425, Spectrum Technologies, Inc, USA) and soil moisture (Watermark soil moisture sensor 6450WD, Spectrum Technologies, Inc, USA) were measured every hour in each stand and the data was stored with a data logger (WatchDog 1425, Spectrum Technologies, Inc, USA).

For estimation of the Rs and Rh fluxes, individual models (3) were developed for each stand for the study period (May-November):

$$\mathrm{Flux} = R_{10}Q_{10}^{((Ts-10)/10)} \quad (3)$$

where R_{10} is respiration rate at temperature 10 °C, Q_{10} represents the relative increase of respiration with a temperature increase of 10 °C, Ts is soil temperature (°C). The cumulative Rs and Rh fluxes were modelled by using daily Ts values calculated from the data loggers. The cumulative Rh flux was corrected for increased decomposition of the severed fine roots and for lack of fresh inputs of intact roots caused by trenching (Epron, 2009), and an approximate decay constant of 0.20 yr^{-1} was used (unpublished data of K. Lõhmus). Since we did not measure the respiration fluxes from December to April, we increased the cumulative flux for the snow-free season (May-November) by 10% (based on closed static chamber measurements, unpublished data of M. Maddison) to calculate the total annual cumulative flux.

2.8. Carbon budget

The C budget for downy birch stands of different ages was compiled by synthesizing the data of above- and belowground biomass production as well as the data of heterotrophic respiration (Rh). Net primary production (NPP) was calculated by summing the annual increments of the aboveground ecosystem compartments (trees, understorey) and the annual increment of the belowground ecosystem compartments (coarse root system, fine roots, roots of the herbaceous understorey).

The estimate for net ecosystem production (NEP) was obtained by subtracting heterotrophic respiration (Rh) from net primary production (NPP) (4) (Clark et al., 2001; Lovett et al., 2006; Meyer et al., 2013):

$$\mathrm{NEP} = \mathrm{NPP} - \mathrm{Rh} \quad (4)$$

The NEP presents the rate at which carbon is accumulated in or emitted from the ecosystem, and is the main parameter characterizing the forest carbon sink or source (Chapin et al., 2006; Waring and Running, 2007).

2.9. Chemical analysis

To analyse the soil as well as the plant material for C content in the oven-dried samples, the dry combustion method was applied using with a varioMAX CNS elemental analyser (ELEMENTAR, Germany). For analysis of N (Kjeldahl) in the soil samples, Tecator ASN 3313 was employed. Available P and K were extracted with ammonium lactate (0.1 *M* NH4CH3CH(OH)COO– 187 + 0.4*M* CH3COOH, pH 3.75). Available phosphorus in the extraction solution was determined by flow injection analysis with the use of the Tecator ASTN 9/84 and the content of available potassium was determined from the same solution by the flame photometric method. Available (exchangeable) Ca and Mg were determined by using the 1 mol L-1 191 NH4OAc extracting solution buffered at pH 7. Soil magnesium content was determined by flow injection analysis with the Tecator ASTN 90/92. Calcium was determined from the same solution by the flame photometric method. The analyses were carried out at the Biochemistry Laboratory of the Estonian University of Life Sciences.

2.10. Statistical analysis

Normality of variables was checked by Lilliefors' and Shapiro-Wilk's tests on the datasets. The *t*-test for independent samples by groups was employed to compare the means for the groups/stands. Linear, non-linear and allometric models were employed for estimating relationships. The measure of the fit of the models was based on the adjusted coefficient of determination (R^2) and on the level of probability (P).

Soil respiration data were log-transformed to normalize them for statistical analysis. To test the effect of trenching and stand age on Rs or Rh, repeated measures ANOVA was performed using the general linear model (GLM) procedure. In the case of significant effects, the means were compared with Tukey's HSD test. *T*-test was used to identify significant differences in Ts and soil moisture between the stands and between control and trenched plots for each stand. A multilinear regression, where soil temperature and moisture were the two independent variables, was employed to examine the relationships between respiration rates and environmental factors (Ts and soil moisture). Further, Pearson correlation coefficient for Rs and soil moisture was calculated; to eliminate the confounding effect of Ts, partial correlation analysis was used. There was negative correlation between Ts and soil moisture for Rs and Rh. To eliminate the effect of temperature on the measured respiration rates, regression Eq. (3) was found for each stand and treatment using monthly average respiration rates and temperatures. Temperature-normalized respiration values were calculated from the regression as the difference between measured and estimated respiration at an observed temperature curve, divided by measured respiration, and the result was plotted against average monthly soil moisture.

In all cases the level of significance $\alpha = 0.05$ was accepted. The software STATISTICA 7.0 (StatSoft Inc.) was employed.

3. Results

3.1. Carbon storages and accumulation in trees

3.1.1. Aboveground biomass and production

The general allometric model (1) described well both the aboveground biomass and the stem mass of the downy birch trees on the basis of breast height diameter (Fig. 1). However, for better estimation, individual parameters of the model were used for each stand (Table 3). The share of stem mass in the total aboveground biomass of the model trees was very stable, ranging between 84 and 87%.

Both the current annual increment (CAI) and the mean annual increment (MAI) of the stemwood demonstrated higher values for the youngest stands and a considerable decrease for the old stand (Table 4).

The weighted average C concentration of aboveground woody biomass for the studied downy birch stands was 47.6%. Variation in the C concentrations of the different fractions of the downy birch trees ranged between 47 and 51%, being the highest (51.0%) in the twigs and the lowest (47.0%) in the stemwood (*t*-test) (Table 5). The corresponding C concentration values were used for calculation of the C fluxes and storages.

Production and C accumulation in woody biomass was the most intensive in the young and middle-aged stands (Table 6). However, the C storage in woody biomass increased markedly with stand age (Table 4). The estimated average stemwood density of downy birch

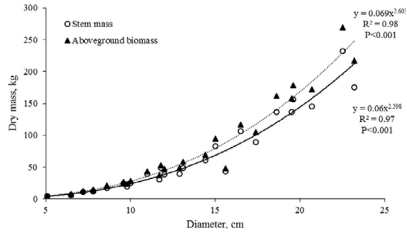


Fig. 1. The regression model of aboveground woody biomass and stem mass on the basis of the downy birch model trees (n = 26).

was 532 ± 1.9 kg m^{-3}, being significantly higher in the oldest stand (605 ± 1.1 kg m^{-3}), (*t*-test, P < 0.01) (Table 4).

3.1.2. Coarse root biomass and production

The coarse root biomass (CRB) of an average model tree in the 30-year-old downy birch stand was 26.2 kg. The stump core and the roots with the largest diameter (d ≥ 10 mm) accounted for 27% and 56% of total CRB, respectively. The corresponding shares of the root fractions 5 ≤ d < 10 mm and 2 ≤ d < 5 mm, were similar (7% and 6%, respectively). As the leafless AGB of an average model tree was 95 kg, the share of the belowground part in aboveground woody biomass accounted for 28%. This root-shoot ratio for an average model tree was applied for calculation of the total CRB of the stands (Table 4).

3.2. Annual carbon flux from fine roots, herbaceous understorey and aboveground litter

Fine root biomass (FRB) was of the same magnitude across the studied stands, being roughly 1.5 t ha^{-1}, except for the oldest stand (DB-78) (Table 7). Neither FRB nor fine root production (FRP) was dependent on stand age (ANOVA, P = 0.99 and P = 0.12, respectively).

Although stand density was lower in the oldest stand, its FRB was of the same magnitude as in the other stands. Thus average FRB per tree increased in the older stands (Fig. 2).

Fine root turnover rate varied between 1 and 2 yr^{-1} for the studied stands, which indicates that the total fine root biomass is renewed during one year. The C concentration did not differ significantly between the fine and coarse roots and the stemwood (Table 5) and the annual C flux into soil via decomposing fine roots was roughly 1 t C ha^{-1} yr^{-1}, except for DB-38.

The biomass of the herbaceous understorey plants decreased with stand age (R = 0.88; P < 0.05). The belowground to aboveground biomass ratio was variable for the stands of different ages (Table 7).

Average C concentration in the above- and belowground biomass of the herbaceous plants was 43.5% and 46.2%, respectively.

The annual C flux into soil via litterfall was of the same magnitude in all stands, being the smallest in the oldest stand (Table 7). The litter flux was the largest in the 30-year-old stand but differed statistically only from that of the oldest stand (Tukey test; P < 0.05).

Leaf litter formed the main share of the organic C flux into soil; the proportion of the branches was modest in all stands. The average C concentration of leaf litter over the whole study period was 49.6%. Thus taking roughly 50% for average C concentration in this case should be relevant.

3.3. Soil respiration and microclimate

The seasonal dynamics (from May to November) of soil temperature (Ts) was quite similar for all studied stands (data not shown). The lowest mean monthly Ts across all stands was in November and the highest in August. Trenching did not affect Ts.

Throughout the growing season, soil moisture fluctuated roughly between 20% and 60% in the studied stands, except for July in the 38- and 78-year-old stands where the soil was drier compared with the other stands (P < 0.05); in May the soil of the youngest stand was saturated with water and its moisture was markedly higher than the soil of other stands (P < 0.05) (Fig. 3).

Regarding the different stands, the soil was drier in the 38- and 78-year-old stands (23 ± 2.1% and 32 ± 3.1%, respectively) compared with the 12-, 24-, and 30-year-old stands (50 ± 4.4%, 46 ± 1.9% and 53 ± 1.6%, respectively) (P < 0.05). Soil moisture was similar in the control and trenched plots in the 24- and 30-year-old stands. In the 12-, 38- and 78-year-old stands, soil moisture was higher in the trenched plots than in the control plots (P < 0.05). However, among these stands, the moisture values improved the regression model only in the case of the youngest stand.

The seasonal dynamics of Rs and Rh showed a similar pattern in all stands following changes in Ts (Fig. 4).

The respiration rates peaked in July at the time of maximum temperature and declined in autumn; mean Rs (May-November) ranged from 0.75 ± 0.06 to 11.16 ± 1.36 μmol CO_2 m^{-2} s^{-1} and Rh ranged from 0.55 ± 0.06 to 5.93 ± 0.16 μmol CO_2 m^{-2} s^{-1} across all stands. Because of an extraordinarily cold period in June, the soil CO_2 effluxes declined in all stands; the measured values in June were similar to the values usually measured in October.

The CO_2 efflux was different between the stands; measured respiration rates in the 24-year-old stand tended to be lower compared to the other stands, however, a significant difference in Rs rates was found only between the 24-year-old and the 30-year-old stands (3.20 ± 0.54 μmol CO_2 m^{-2} s^{-1} versus 4.14 ± 0.74) (P < 0.05). Also mean Rh was significantly lower in the 24-year-old stand than in the 30- and 38-year-old stands (2.14 ± 0.34 μmol CO_2 m^{-2} s^{-1} versus 2.52 ± 0.41 and 2.75 ± 0.45 μmol CO_2 m^{-2} s^{-1} (P < 0.05). No significant difference was found in the respiration rates between the other stands. Cumulative annual Rs was 7.4–8.8 t C ha^{-1} yr^{-1} and cumulative annual Rh was 4.7–6.2 t C ha^{-1} yr^{-1}, with the highest values for the middle-aged stands (Table 8). At the same time, mean soil C

Table 4
Biomass and production of the downy birch stands of different ages growing on drained *Histosols*. AGB – aboveground woody biomass, CRB – coarse root biomass, MAI – mean annual increment of stems, CAI – current annual increment of stems. Superscript letters indicate significant differences in stemwood density (*t*-test, P < 0.05).

Stand	Stems	Branches	Shoots	AGB	CRB	Stemwood density, g cm^{-3}	Stand volume, m^3 ha^{-1}	MAI	CAI
	t ha^{-1}							m^3 ha^{-1} yr^{-1}	
DB-12	38.7	6.3	0.92	45.9	12.9	0.503 [a]	76.9	6.41	9.82
DB-24	59.4	8.3	0.97	68.7	19.2	0.512 [a]	116.0	4.84	7.94
DB-30	103.7	13.7	1.22	118.6	33.2	0.538 [a]	192.7	5.07	8.31
DB-38	64.3	11.2	0.80	76.3	21.4	0.504 [a]	127.6	4.25	6.06
DB-78	93.4	12.9	0.74	107	30.0	0.605 [b]	154.4	1.98	2.84

Table 5
Mean carbon concentration in the different biomass fractions of the downy birch. Superscript letters indicate significant differences between the fractions (*t*-test, $P < 0.05$).

Fraction		C, %
Stemwood		47.0[a]
Stembark		51.0[b]
Branches (wood + bark)		48.6[a]
Twigs		51.6[b]
Fine roots	d < 2 mm	49.1[a]
Coarse roots	d = 2–5 mm	48.2[a]
	d = 5–10 mm	47.8[a]
	d > 10 mm	47.3[a]
Stump core		47.6[a]

emission did not differ significantly between the stands of different ages (ANOVA, *t*-test $P > 0.05$). The relative contribution of Rh to Rs varied between 0.60 and 0.70 irrespective of stand age (Table 8).

Soil temperature was the main driver of seasonal variation in both Rs and Rh and described 68–92% of the variation in the respiration rates in the control and trenched plots. The temperature sensitivity (Q_{10} value) of both Rs and Rh ranged from 3.0 to 5.5, showing the highest values in the 78-year-old stand (Table 8). Considering increased soil moisture for some stands in the trenched plots, we used partial correlation to eliminate the confounding effect of Ts and found that soil moisture had a negative effect on the soil CO_2 effluxes. Still, a significant effect of moisture on Rh was only noted for the 12- and 24-year-old stands ($r = -0.79$ and -0.65, respectively, $P < 0.05$). For the other stands, the effect of soil moisture was weak. Furthermore, regarding all stands, there was no significant relationship between normalized respiration rates and soil moisture for Rs and for Rh (Fig. 5).

3.4. Carbon budgets

The values of the net ecosystem production (NEP) in the downy birch stands decreased from the youngest to the oldest stand (from +3 to -0.95 t C ha^{-1} yr^{-1}) (Table 9).

The C was primarily accumulated in tree biomass and the largest C input flux into the soil originated from aboveground litter. Both the aboveground and belowground litter (FRP) fluxes were of the same magnitude in all studied stands and the C input through the annual production of the herbaceous understorey plants was modest (Table 9).

The annual heterotrophic soil respiration (Rh) flux exceeded the annual organic C input into the soil (Table 9) in all stands irrespective of stand age or depth of the soil organic layer. This indicates continuous mineralization of peat and a decrease of the soil C storage.

4. Discussion

4.1. Carbon accumulation in woody biomass

The growth pattern of the studied downy birch stands demonstrated intensive biomass production at the young stage and decreasing increment with increasing stand age (Table 6), which is a common dynamic forest growth pattern. Stand volume peaked in the 30-year-old stand with a standing volume of 193 m^3 ha^{-1}, the volume of the 24-year-old birch stand was already 116 m^3 ha^{-1} (Table 4). Hytönen and Aro (2012) reported aboveground biomass (AGB) values of 62 and 212 t ha^{-1} for 21- and 37-year-old downy birch stands growing on cutaway peatland, respectively. In the present study, the mean annual stemwood increment (MAI) of the stands was between 4.2–6.4 m^3 ha^{-1} yr^{-1} for the young and middle-age of stands (Table 4), which can be considered a high value for downy birch. In Sweden, the MAI of downy birch stands growing on abandoned agricultural lands varied between 0.5–4.4 t ha^{-1} yr^{-1} (Johansson, 1999). A high annual biomass production (4.1–6.5 t ha^{-1} yr^{-1}) of intensively fertilized downy birch stands (aged 6–19-years) growing on cutaway peatland was reported by Hytönen and Saarsalmi (2009).

Local yield tables for downy birch from an earlier period are missing in Estonia, which can be explained by the low economic and silvicultural value of this species. There is only one publication comparing the diameter increment of silver birch with that of downy birch (Henno, 1963). At the same time, yield tables of downy birch stands growing on drained peatlands are available in Finland (Saramäki, 1977) and development of downy birch stands after drainage in various peatlands in Finland was simulated by Minkkinen et al. (2002).

We established a strong correlation ($R^2 > 0.97$; $P < 0.001$) between breast height diameter and woody AGB or stem mass (Fig. 1), which serves as a good basis for compiling country-specific general downy birch growth models. The average value of stemwood density for downy birch, found in the present study was lower than the corresponding values reported for silver birch in Estonia (0.65 g cm^{-3}) (Kasesalu, 1965).

Although an average C concentration of 50% in dry mass is normally used to calculate C accumulation in woody biomass, several studies (Laiho and Laine, 1997; Bert and Danjon, 2006; Zhang et al., 2009) have demonstrated that the C concentration of different tree species and in different woody biomass fractions may vary in a broad range (44–56%). The weighted average C concentration in woody biomass found in the present study, at 48%, was slightly lower than that reported in a similar Finnish study at 49.3% (Hytönen and Aro, 2012).

Roots are essential contributors to NPP and play an important role in the C cycling of all forest ecosystems (Prescott et al., 2016). However, empirical data of the belowground coarse root biomass of birch are rare, with only a few available papers (Repola, 2008; Varik et al., 2013; Hunziker et al., 2014). However, one should not forget that several factors may affect the root-shoot ratio (Cairns et al., 1997) and trees growing in peatlands may allocate more biomass to the belowground parts than trees growing on mineral soils (Laiho and Finér, 1996). This was also confirmed in our study: the share of the roots (28%) in the middle-aged downy birch stand was higher than the corresponding share (21%) in a silver birch stand of similar age growing on mineral soil (Varik et al., 2013).

Table 6
Annual carbon accumulation in the woody biomass production of the downy birch trees.

Stand	Annual production, t ha^{-1} yr^{-1}				Accumulation, t C ha^{-1} yr^{-1}			
	Branches + twigs	Stems	Coarse roots	Total	Branches + twigs	Stems	Coarse roots	Total
DB-12	1.73	6.27	1.64	9.64	0.87	2.97	0.79	4.63
DB-24	1.54	5.13	1.32	7.98	0.77	2.43	0.63	3.83
DB-30	1.58	4.89	1.48	7.95	0.79	2.32	0.71	3.82
DB-38	1.62	3.66	0.98	6.26	0.81	1.73	0.47	3.02
DB-78	0.98	2.53	0.55	4.06	0.49	1.20	0.27	1.95

Table 7
Annual carbon flux into the soil through the annual production of fine roots, herbaceous understorey and aboveground litter. Fine root biomass (FRB) and fine root production (FRP) represent the upper 0–40 soil layer. AG – aboveground; BG – belowground.

Stand	Fine roots of downy birch					Herbaceous understorey		Aboveground litter	
	FRB, t ha^{-1}	FRP, t ha^{-1} yr^{-1}	Turnover rate, yr^{-1}	Longevity, yr	Flux, t C ha^{-1} yr^{-1}	Flux, t C ha^{-1}			
						AG	BG	Leaf litter	Total AG litter
DB-12	1.37	1.81	1.32	0.76	0.89	0.14	0.43	1.63	1.70
DB-24	1.50	2.17	1.44	0.69	1.07	0.19	0.19	1.50	1.55
DB-30	1.42	2.42	1.71	0.58	1.19	0.17	0.08	1.65	1.91
DB-38	1.48	3.02	2.04	0.49	1.48	0.10	0.07	1.62	1.87
DB-78	1.95	1.88	0.96	1.04	0.92	0.05	0.05	1.17	1.50

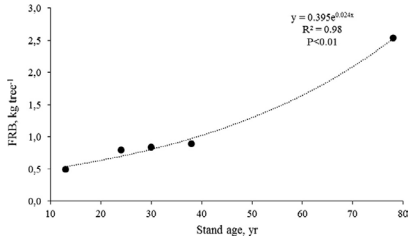


Fig. 2. Fine root biomass per tree in the downy birch stands of different ages.

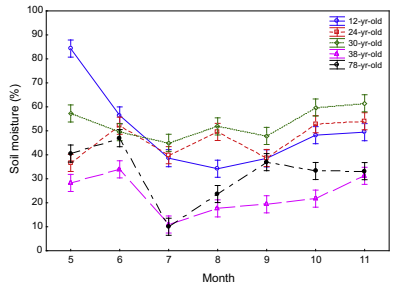


Fig. 3. Seasonal dynamics of soil moisture (%) in the downy birch stands from May to November 2014. Error bars represent the standard error of the means.

4.2. Above- and belowground litter flux

The annual aboveground litter flux was of the same magnitude in all studied stands, except for the oldest stand (DB-78), which can be explained by lower stand density (Table 1). In deciduous stands, both foliage mass and leaf area increase during the early developmental stage until reaching optimal level and stabilizing thereafter. In studied stands leaf mass stabilized at optimal level already in the 12-year-old stand, i.e. at a quite early stage. For fast growing silver birch and grey alder stands, this occurs at age between 5 and 10 years (Uri et al., 2012; Rytter and Rytter, 2016).

Although fine root (d < 2 mm) biomass (FRB) formed a quite small share in the total biomass of trees (Brunner and Godbold, 2007), they contributed significantly to C cycling in forest ecosystems (Gill and Jackson, 2000; Finér et al., 2011). The contribution of fine roots depends on many factors among them stand age and soil type (Finér et al., 1997; Vanninen and Mäkelä, 1999; Ostonen et al., 2011). In the present study the FRB of downy birch was of the same magnitude in all stands irrespective of age (Table 7). The largest share of FRB was located in the upper 0–10 cm soil layer in all cases, which is a very typical pattern for various forests (Finér et al., 2007; Helmisaari et al., 2007) owing to the larger nutrient pool in the topsoil (Ostonen et al., 2005; Garkoti, 2010).

The annual fine root production (FRP) of the studied stands was high (1.8–3 t ha^{-1} yr^{-1}) and did not depend on stand age (Table 7). Because of high FRP, average fine root longevity was low and turnover was fast. Turnover rate varied between 1 and 2 yr^{-1}, which was significantly higher than that estimated for silver birch on mineral soils (0.5–0.7 yr^{-1}) (Varik et al., 2015). An average fine root turnover rate of 1.0 yr^{-1} for European broad-leaved summergreen trees has been used in biogeochemical models (Brunner et al., 2013). However, Rytter (2013) has found that quite a large part of short-living finest roots (<1 mm) may have very high turnover rate (5–6 yr^{-1}). Thus despite the high turnover rate, the annual C input into soil via fine root litter may be even underestimated since we sampled the root meshes once per year, in October, while FRP peaked in summer (Aosaar et al., 2013; Rytter, 2013; Varik et al., 2015).

In a study of Meyer et al. (2013) it was assumed that annual FRP is a steady state C flux into the soil. The production, dying and decomposition of fine roots in closed canopy forests are continuous long lasting processes and FRP is a steady state C flux into the soil. A similar approach was also applied in our earlier studies (Uri et al., 2011, 2017; Varik et al., 2015).

4.3. Carbon budget

The studied downy birch stands growing on drained fertile peat soils acted as C sinks at the young and middle-age stages, reaching an almost steady state in the pre-mature age and acting as a C source at the over-mature stage. The oldest stand turned to a C source due to decreased woody biomass production. At the same time the C efflux (Rh) was roughly similar in all studied stands. The estimated annual Rh efflux (4.7–6.2 t C ha^{-1}) was close to the upper limit of the reported values for organic soils, at 1.5–6.7 t C ha^{-1} yr^{-1} (Minkkinen et al., 2007; Ojanen et al., 2010). A larger flux, at 8.1 t C ha^{-1} yr^{-1}, reported by Meyer et al. (2013), was recorded for spruce forest on fertile peatland. A high Rh flux from the studied stands was expected since after drainage water level decreases and deeper soil layers become available for aerobic heterotrophic degradation (Berg and McClaugherty, 2003; von Arnold et al., 2005a). Moreover, birch leaf litter is a readily degradable substrate (Berg and Laskowski, 2006) and can considerably contribute to total annual Rh (Janssens et al., 2001). Despite the high potential of drained *Histosols* to Rh, the estimated annual Rh flux was of same magnitude as that estimated for forests

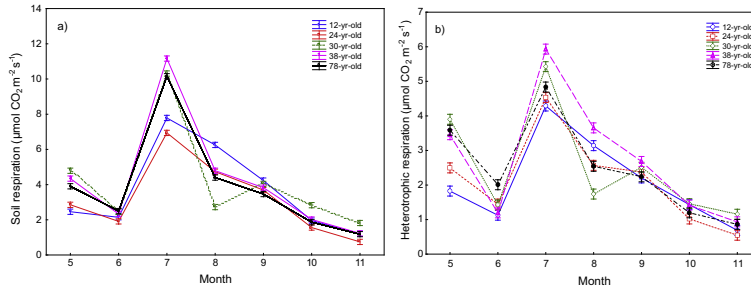


Fig. 4. Seasonal dynamics of (a) total soil respiration (Rs, µmol CO_2 m^{-2} s^{-1}) and (b) heterotrophic respiration (Rh, µmol CO_2 m^{-2} s^{-1}) in the downy birch stands from May to November 2014. Error bars represent the standard error of the means.

Table 8
Annual total soil respiration (Rs), heterotrophic respiration (Rh), Rh/Rs ratio (calculated for the period May-November) and the Q_{10} values for the studied downy birch stands growing on drained *Histosols*.

Stand	Rs, t C ha^{-1}	Rh, t C ha^{-1}	Rh/Rs	Q_{10}	
				Rs	Rh
DB-12	7.9	4.7	0.60	4.3	3.9
DB-24	7.4	5.1	0.70	4.8	4.7
DB-30	8.7	5.5	0.63	3.0	3.0
DB-38	8.8	6.2	0.70	4.4	3.9
DB-78	7.4	5.1	0.69	5.5	5.2

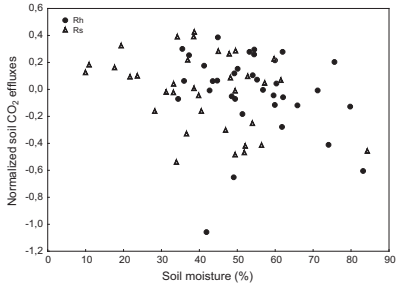


Fig. 5. Relationship between temperature-normalized respiration and soil moisture across all data.

growing on mineral soils in Estonia (Varik et al., 2015; Kukumägi et al., 2017; Uri et al., 2017). This may be the consequence result of long lasting drainage; probably the peak of decomposition of peat is over and the annual Rh flux is stabilized.

Soil temperature was the dominating environmental factor that influenced the seasonal dynamics of Rs and Rh (Minkkinen et al., 2007; Mäkiranta et al., 2008, 2009) and described 68–92% of the variation in the respiration rates. In the current study, the temperature sensitivity (Q_{10} value) of both of Rs and Rh remained in the range reported for peatlands (2.2–4.9) (Bubier et al., 1998; Lafleur et al., 2005; Acosta et al., 2017). Only the oldest stand had higher Q_{10} values. In comparison, the Q_{10} values of Rh were lower in silver birch stands on mineral soils in the years with a dry summer (1.9–3.0) (Varik et al., 2015). Organic soils have a great potential to lose C with increasing temperature (Kirschbaum, 1995; Rustad et al., 2001; Wu et al., 2011), contributing thereby to a positive feedback to the greenhouse effect (Bellamy et al., 2005) and thus estimation of Rh and calculation of the Q_{10} values of Rh for peatland soils is especially important (Gorham, 1991). Aguilos et al. (2013) found that soil warming in cool-temperate forested peatland increased Rh and Q_{10} values attributing the increase to high substrate availability and high soil water content.

The C balance of a forest stand can significantly change with ageing (Kolari et al., 2004). Old stands can become weak C sinks or even sources of C (Goulden et al., 1996; Lindroth et al., 1998) since their annual biomass production decreases, i.e. C emission through soil Rh exceeds the C input, which was also obvious in our study. In forests growing on drained organic soils, the high C uptake by trees can often compensate for intensive Rh (Minkkinen et al., 2002; Hargreaves et al., 2003). Since young downy birch stands act as a C sink owing to the intensive annual biomass production of the trees, management of such forests, using optimal rotation length, is essential in terms of effective C accumulation. The recommended rotation length for downy birch stands is usually 50–60 years (Niemistö et al., 2008) and thus a 78-year-old stand is over-mature. The maximum rotation length for downy birch is 70–80 years considering its biological ageing, with decreased growth and an increased risk of rot (Hynynen et al., 2010). Further, reforestation of these areas after clear-cut by more productive tree species like black alder (*Alnus glutinosa*) or Norway spruce (*Picea abies*) would be a one reasonable option. At same time, despite their high productivity, spruce stands on organic soils may be sensitive to wind throw.

The organic C input to the soil from above- and belowground litter was appreciable in all stands accounting for 36–56% of NPP. However, the relative share of the total litter C input in total NPP

Table 9
Carbon input and output fluxes and net ecosystem production (NEP) in the downy birch stands growing on *Histosols*.

Flux, t C ha^{-1} yr^{-1}	Stand				
	DB-12	DB-24	DB-30	DB-38	DB-78
Plant aboveground					
(1) Leafless tree biomass increment	3.84	3.20	3.11	2.55	1.69
(2) Leaf litter	1.63	1.50	1.65	1.62	1.17
(3) Herbaceous understorey production	0.14	0.19	0.17	0.10	0.05
Plant belowground					
(4) Coarse root biomass increment	0.79	0.63	0.71	0.47	0.27
(5) Tree fine root production	0.89	1.07	1.19	1.48	0.92
(6) Understorey root and rhizome production	0.43	0.19	0.08	0.07	0.05
Soil					
(7) C output (Heterotrophic respiration)	4.7	5.1	5.5	6.2	5.1
(8) C input = (2) + (3) + (5) + (6)	3.09	2.95	3.09	3.27	2.19
(9) Soil C exchange = (8) − (7)	−1.61	−2.15	−2.41	−2.93	−2.91
Productivity					
(10) NPP = (1) + (2) + (3) + (4) + (5) + (6)	7.72	6.78	6.91	6.29	4.15
(11) NEP = (10) − (7)	3.02	1.68	1.41	0.09	−0.95

increased in the older stands. The contribution of the understorey vegetation to NPP was modest and decreased in the older stands. The annual Rh flux exceeded the organic C input into the soil (litter) in all studied stands (Table 9), which indicated soil C loss. However, site fertility can play a crucial role from this aspect as in nutrient poor drained peatland C accumulates in soil as dead organic matter (Lohila et al., 2011). The effect of the site type and trophic level on the C balance is poorly studied; average C loss from drained peatlands in the southern and middle boreal vegetation zones of central Finland is estimated at 150 g C m^{-2} yr^{-1} (Simola et al., 2012).

Moreover, to estimate the total effect of drainage on atmosphere and climate changes, the emissions of other greenhouse gases (GHG) should be taken into account because they may change balances in terms of the potential of global warming. In the present study, methane (CH_4) and N_2O emissions from the soil were not measured. We assume that methane emission was modest as it is usually decreased in drained soils (von Arnold et al., 2005a, 2005b; Ilomets, 1996; Martikainen et al., 1993; Salm et al., 2009). According to Meyer et al. (2013), CH_4 emission was very low and negative in a fertile drained organic soil under a Norway spruce stand in all cases. However, fluctuations in groundwater level may significantly increase CH_4 emission (Mander et al., 2015).

The more powerful greenhouse gas (N_2O) emission may be also appreciable, still studies in forestry drained peatlands demonstrated modest source of N_2O (Ojanen et al., 2010; Lohila et al., 2011). Regarding the other GHG, more detailed further studies are needed.

5. Conclusions

The young and middle-aged downy birch stands growing on drained fertile *Histosols* acted as effective C sinks. The NEP in the 38-year-old stand was roughly zero, indicating that such ecosystems are almost C neutral. The over-matured downy birch stand was a C emitting ecosystem, i.e. a C source. Thus, in terms of more effective C accumulation, optimization of rotation length for management of downy birch stands on drained swamps may be an essential issue.

The annual Rh flux was relatively similar in the studied stands and did not depend on stand age or depth of the peat layer. The annual organic C input into the soil (above- and belowground litter, understorey vegetation) was smaller than the annual Rh flux irrespective of stand age, indicating continuous mineralization of peat and a decrease in the soil C pool. The soil C pool was the main C storage in drained downy birch ecosystems and the C accumulated in the woody biomass of the trees accounted for only 5–20% of the total ecosystem's C pool.

Acknowledgements

This study was supported by the projects of the Institutional Research Funding IUT21-04 and IUT34-9 of the Estonian Ministry of Education and Research as well as by the Environmental Investment Centre project No. 5725 and by the project of the Estonian Forest Management Centre No 1-18/113 (T13072MIMK). We thank Mrs. Ester Jaigma for revising the English text of the manuscript.

References

Acosta, M., Juszczak, R., Chojnicki, B., Pavelka, M., Havránková, K., Lesny, J., et al., 2017. CO_2 fluxes from different vegetation communities on a peatland ecosystem. Wetlands 1–13. http://dx.doi.org/10.1007/s13157-017-0878-4.

Aguilos, M., Takagi, K., Liang, N., Watanabe, Y., Teramoto, M., Goto, S., et al., 2013. Sustained large stimulation of soil heterotrophic respiration rate and its temperature sensitivity by soil warming in a cool-temperate forested peatland. Tellus B 65. http://dx.doi.org/10.3402/tellusb.v65i0.20792.

Ahti, T., Hamet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in northwestern Europe. Ann. Bot. Fennici 5, 169–211.

Aosaar, J., Varik, M., Lõhmus, K., Ostonen, I., Becker, H., Uri, V., 2013. Long-term study of above- and belowground biomass production in relation to nitrogen and carbon accumulation dynamics in a grey alder (*Alnus incana* (L.) Moench) plantation on former agricultural land. Eur. J. For. Res. 132 (5–6), 737–749. http://dx.doi.org/10.1007/s10342-013-0706-1.

Aosaar, J., Mander, Ü., Varik, M., Becker, H., Morozov, G., Maddison, M., et al., 2016. Biomass production and nitrogen balance of naturally afforested silver birch (Betula pendula Roth.) stand in Estonia. Silva Fennici 50 (4), 1–19. http://dx.doi.org/10.14214/sf.1628.

Bellamy, P.H., Loveland, P.J., Bradley, R.I., Lark, R.M., Kirk, G.J., 2005. Carbon losses from all soils across England and Wales 1978–2003. Nature 437, 245–248. http://dx.doi.org/10.1038/nature04038.

Berg, B., Laskowski, R., 2006. Litter decomposition: a guide to carbon and nutrient turnover. In: Litter Decomposition: A Guide to Carbon and Nutrient Turnover, first ed. Advances in Ecological Research 38. Elsevier Academic Press, UK.

Berg B, McClaugherty C. 2003. Plant litter. decomposition, humus formation, carbon sequestration. Springer, Berlin Heidelberg New York.

Bert, D., Danjon, F., 2006. Carbon concentration variations in the roots, stem and crown of mature *Pinus pinaster* (Aait.). Forest Ecol. Manage. 222, 279–295. http://dx.doi.org/10.1016/j.foreco.2005.10.030.

Birdsey, R., Pan, Y., 2015. Trends in management of the world's forests and impacts on carbon stocks. Forest Ecol. Manage. 355, 83–90. http://dx.doi.org/10.1016/j.foreco.2015.04.031.

Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320, 1444–1449. http://dx.doi.org/10.1126/science.1155121.

Bormann, B.T., Gordon, J.C., 1984. Stand density effects in young red alder plantations: productivity, photosynthate partitioning and nitrogen fixation. Ecology 2, 394–402. http://dx.doi.org/10.2307/1941402.

Brunner, I., Godbold, D.L., 2007. Tree roots in a changing world. J. For. Res. 12, 78–82. http://dx.doi.org/10.1007/s10310-006-0261-4.
Brunner, I., Bakker, M.R., Björk, R.G., Hirano, Y., Lukac, M., Aranda, X., et al., 2013. Fine-root turnover rates of European forests revisited: an analysis of data from sequential coring and ingrowth cores. Plant Soil 362, 357–372. http://dx.doi.org/10.1007/s11104-012-1313-5.
Bubier, J.L., Crill, P.M., Moore, T.R., Savage, K., Varner, R.K., 1998. Seasonal patterns and controls on net ecosystem CO_2 exchange in a boreal peatland complex. Global Biogeochem. Cycles 12, 703–714. http://dx.doi.org/10.1029/98GB02426.
Cairns, M., Brown, S., Helmer, E., Baumgardner, M., 1997. Root biomass allocation in the world's upland forests. Oecologia 111, 1–11. http://dx.doi.org/10.1007/s004420050201.
Chapin, F.S., Woodwell, G.M., Randerson, J.T., Rastetter, E.B., Lovett, G.M., Baldocchi, D.D., et al., 2006. Reconciling carbon-cycle concepts, terminology, and methods. Ecosystems 9 (7), 1041–1050. http://dx.doi.org/10.1007/s10021-005-0105-7.
Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J., 2001. Measuring net primary production in forests: concepts and field methods. Ecol. Appl. 11 (2), 356–370. http://dx.doi.org/10.2307/3060894.
Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Texler, M.C., Wisniewski, J., 1994. Carbon pools and fluxes of global forest ecosystems. Science 263, 185–190. http://dx.doi.org/10.1126/science.263.5144.185.
Epron, D., 2009. Separating autotrophic and heterotrophic components of soil respiration: lessons learned from trenching and related root-exclusion experiments. In: Kutsch, W.L., Bahn, M., Heinemeyer, A. (Eds.), Soil Carbon Dynamics: An Integrated Methodology. Cambridge University Press, UK, pp. 157–168.
Estonian Environmental Information Centre. 2013. Aastaraamat Mets 2013. Yearbook Forest 2013. Tartu 2014 (in Estonian).
Finér, L., Messier, C., Granpré, L., 1997. Fine-root dynamics in mixed boreal conifer – broad-leafed forest stands at different successional stages after fire. Can. J. Forest Res. 27, 304–314. http://dx.doi.org/10.1139/x96-170.
Finér, L., Helmisaari, H.-S., Lõhmus, K., Majdi, H., Brunner, I., Børja, I., Eldhuset, E., Godbold, D., et al. 2007. Variation in fine root biomass of three European tree species: Beech (Fagus sylvatica L.), Norway spruce (Picea abies L. Karst.) and Scots pine (Pinus sylvestris L.). Plant Biosyst. 141, 394–405. dx.doi.org/10.1080/11263500701625897.
Finér, L., Ohashi, M., Noguchi, K., Hirano, Y., 2011. Factors causing variation in fine root biomass in forest ecosystems. Forest Ecol. Manage. 261, 265–277. http://dx.doi.org/10.1016/j.foreco.2010.10.016.
Garkoti, S.C., 2010. Fine root dynamics in three central Himalayan high elevation forests ranging from closed canopied to open-canopied treeline vegetation. J. For. Res.-Jpn 16 (2), 136–143. http://dx.doi.org/10.1007/s10310-010-0218-5.
Gill, R.A., Jackson, R.B., 2000. Global patterns of root turnover for terrestrial ecosystems. New Phytol. 147, 13–31. http://dx.doi.org/10.1046/j.1469-8137.2000.00681.x.
Gorham, E., 1991. Northern Peatlands: Role in the carbon cycle and probable responses to climatic warming. Ecol. Appl. 1, 182–195. http://dx.doi.org/10.2307/1941811.
Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C., Wofsy, S.C., 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. Glob. Change Biol. 2, 159–168. http://dx.doi.org/10.1111/j.1365-2486.1996.tb00070.x.
Gower, S., 2003. Patterns and mechanisms of the forest carbon cycle. Annu. Rev. Environ. Resour. 28, 169–204.
Hargreaves, K.J., Milne, R., Cannell, M.G.R., 2003. Carbon balance of afforested peatland in Scotland. Forestry 76, 299–317. http://dx.doi.org/10.1093/forestry/76.3.299.
Harmon, M.E., Bond-Lamberty, B., Tang, J., Vargas, R., 2011. Heterotrophic respiration in disturbed forests: A review with examples from North America. J. Geophys. Res. 116, G00K04. doi: http://dx.doi.org/10.1029/2010JG001495.
Helmisaari, H.-S., Derome, J., Nöjd, P., Kukkola, M., 2007. Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. Tree Physiol. 27, 1493–1504. http://dx.doi.org/10.1093/treephys/27.10.1493.
Henno, O., 1963. Kasetüvede mahutabel (Silver birch volume table). Transactions of Estonian Agricultural Academy/EPA teaduslike tööde kogumik 41. Tartu, 114–119 (in Estonian).
Hirano, Y., Noguchi, K., Ohashi, M., Hishi, T., Makita, N., Fujii, S., et al., 2009. A new method for placing and lifting root meshes for estimating fine root production in forest eco-systems. Plant Root 3, 26–31. http://dx.doi.org/10.3117/plantroot.3.26.
Houghton, R.A., 2005. Aboveground forest biomass and the global carbon balance. Global Change Biol. 11 (6), 945–958. http://dx.doi.org/10.1111/j.1365-2486.2005.00955.x.
Hunziker, M., Sigurdsson, B.D., Halldorsson, G., Schwanghart, W., Kuhn, N., 2014. Biomass allometries and coarse root biomass distribution of mountain birch in southern Iceland. Icel Agric. Sci. 27, 111–125.
Hynynen, J., Niemistö, P., Viherä-Aarnio, A., Brunner, A., Hein, S., Velling, P., 2010. Silviculture of birch (Betula pendula Roth and Betula pubescens Ehrh.) in northern Europe. Forestry 83(1), pp. 103–119, doi: http://dx.doi.org/10.1093/forestry/cpp035.
Hytönen, J., Saarsalmi, A., 2009. Long-term biomass production and nutrient uptake of birch, alder and willow plantations on cut-away peatland. Biomass Bioenerg. 33, 1197–1211. http://dx.doi.org/10.1016/j.biombioe.2009.05.014.
Hytönen, J., Aro, L., 2012. Biomass and nutrition of naturally regenerated and coppiced birch on cutaway peatland during 37 years. Silva Fennici 46 (3), 377–394.
Hyvönen, R., Persson, T., Andersson, S., Olsson, B., Ågren, G.I., Linder, S., 2007. Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. Biogeochemistry 89, 121–137.
Ilomets, M., 1996. Temporal changes of Estonian peatlands and carbon balance. In: Punning, J.M. (Ed.), Estonia in the System of Global Climate Change. Institute of Ecology, Tallinn, Estonia, pp. 65–75.
Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., et al., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Glob. Change Biol. 7, 269–278. http://dx.doi.org/10.1046/j.1365-2486.2001.00412.x.
Johansson, T., 1999. Biomass equations for determining fractions of *pendula* and *pubecsens* birches growing on abandoned farmland and some practical implications. Biomass Bioenerg. 16, 223–238.
Kaipanen, T., Liski, J., Pussinen, A., Karjalainen, T., 2004. Managing carbon sinks by changing rotation length in European forests. Environ. Sci. Policy 7, 205–219. http://dx.doi.org/10.1371/journal.pone.0115234.
Kasesalu, A., 1965. Kasepuidu füüsikalis-mehaanilistest omadustest erinevates kasvukohatüüpides (The physical and mechanical qualities of silver birch timber growing in different site types). Metsanduslikud Uurimused 4, 149–157 (in Estonian).
Kirschbaum, M.U.F., 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biol. Biochem. 27, 753–760.
Kolari, P., Hari, P., Berninger, F., Pumpanen, J., Rannik, Ü., Ilvesniemi, H., 2004. Carbon balance of different aged Scots pine forests in Southern Finland. Glob. Change Biol. 10, 1106–1119. http://dx.doi.org/10.1111/j.1529-8817.2003.00797.x.
Korjus, H., Pöllumäe, P., Kangur, A., 2015. Why do we need a research and demonstration area of forest management planning at Järvselja? Forest. Studies 63, 151–159. http://dx.doi.org/10.1515/fsmu-2015-0014.
Kukumägi, M., Ostonen, I., Uri, V., Helmisaari, H.-S., Kanal, A., Kull, O., et al., 2017. Variation of soil respiration and its components in hemiboreal Norway spruce stands of different ages. Plant Soil 414, 265–280. http://dx.doi.org/10.1007/s11104-016-3133-5.
Lafleur, P.M., Moore, T.R., Roulet, N.T., Frolking, S., 2005. Ecosystem respiration in a cool temperate bog depends on peat temperature but not water table. Ecosystems 8, 619–629. http://dx.doi.org/10.1007/s10021-003-0131-2.
Laiho, R., Finér, L., 1996. Changes in root biomass after water- level drawdown on pine mires in southern Finland. Scand J. Forest. Res. 11, 251–260. http://dx.doi.org/10.1080/02827589609382934.
Laiho, R., Laine, J., 1997. Tree stand biomass and carbon content in an age sequence of drained pine mires in southern Finland. Forest Ecol. Manage. 93, 161–169.
Leppelt, T., Dechow, R., Gebbert, S., Freibauer, A., Lohila, A., Augustin, J., et al., 2014. Nitrous oxide emission budgets and land-use-driven hotspots for organic soils in Europe. Biogeosciences 11, 6595–6612. http://dx.doi.org/10.5194/bg-11-6595-2014.
Lindroth, A., Grelle, A., Moren, A.S., 1998. Long-term measurements of boreal forest carbon exchange reveal large temperature sensitivity. Glob. Change Biol. 4, 443–450. http://dx.doi.org/10.1046/j.1365-2486.1998.00165.x.
Liski, J., Nissinen, A., Erhard, M., Taskinen, O., 2003. Climatic effects on litter decomposition from arctic tundra to tropical rainforest. Glob Change Biol. 9, 575–584.
Lohila, A., Minkkinen, K., Aurela, M., Tuovinen, J.P., Penttilä, T., Ojanen, P., et al., 2011. Greenhouse gas flux measurements in a forestry-drained peatland indicate a large carbon sink. Biogeosciences 8, 3203–3218. http://dx.doi.org/10.5194/bg-8-3203-2011.
Lõhmus, E., 1984. Eesti metsakasvukohatüübid. Tallinn, p 76 (In Estonian).
Lõhmus, K., Kuusemets, V., Ivask, M., Teiter, S., Augustin, J., Mander, Ü., 2002. Budgets of nitrogen fluxes in riparian grey alder forests. Arch. Hydrobiol. 13 (3–4), 321–332.
Lõhmus, K., Lasn, R., Oja, T., 1991. The influence of climatic and soil physical conditions on growth and morphology of Norway spruce roots. In: Michael, B.L., Persson, H. (Eds.), Plant Roots and their Environment. Elsevier. Development of Agricultural and Managed Forest Ecology, 24, pp. 233–239.
Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. Bioscience 56, 395–405.
Lukac, M., Godbold, D.L., 2010. Fine root biomass and turnover in southern taiga estimated by root inclusion nets. Plant Soil 331, 505–513.
Mander, Ü., Maddison, M., Soosaar, K., Teemusk, A., Kanal, A., Uri, V., et al., 2015. The impact of a pulsing groundwater table on greenhouse gas emissions in riparian grey alder stands. Environ. Sci. Pollut. Res. 22 (4), 2360–2371. http://dx.doi.org/10.1007/s11356-014-3427-1.
Mäkiranta, P., Laiho, R., Fritze, H., Hytönen, J., Laine, J., Minkkinen, K., 2009. Indirect regulation of heterotrophic peat soil respiration by water level via microbial community structure and temperature sensitivity. Soil Biol. Biochem. 41, 695–703.
Mäkiranta, P., Minkkinen, K., Hytönen, J., Laine, J., 2008. Factors causing temporal and spatial variation in heterotrophic and rhizospheric components of soil respiration in afforested organic soil croplands in Finland. Soil Biol. Biochem. 40, 1592–1600. http://dx.doi.org/10.1016/j.soilbio.2008.01.009.

Martikainen, P.J., Nykänen, H., Crill, P., Silvola, J., 1993. Effect of a lowered water table on nitrous oxide fluxes from northern peatlands. Nature 366, 51–53. http://dx.doi.org/10.1038/366051a0.
McClaugherty, C.A., Aber, J.D., Melillo, J.M., 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 635, 1481–1490.
Meyer, A., Tarvainen, L., Nousratpour, A., Björk, R.G., Ernfors, M., Grelle, A., et al., 2013. A fertile peatland forest does not constitute a major greenhouse gas sink. Biogeosciences 10, 7739–7758. http://dx.doi.org/10.5194/bg-10-7739-2013.
Minkkinen, K., Korhonen, R., Savolainen, I., Laine, J., 2002. Carbon balance and radiative forcing of Finnish peatlands 1900–2100 – the impact of forestry drainage. Glob. Change Biol. 8, 785–799.
Minkkinen, K., Laine, J., Shurpali, N.J., Mäkiranta, P., Alm, J., Penttilä, T., 2007. Heterotrophic soil respiration in forestry-drained peatlands. Boreal Environ. Res. 12, 115–126.
Niemistö, P., Viherä-Aarnio, A., Velling, P., Heräjärvi, H., Verkasalo, E. (Eds.), 2008. Koivun kasvatus ja käyttö. Metla & Metsäkustannus, Karisto Oy, Hämeenlinna, Finland, pp. 1–254 (in Finnish).
Ohashi, M., Nakano, A., Hirano, Y., Noguchi, K., Ikeno, H., Fukae, F., et al., 2016. Applicability of the net sheet method for estimating fine root production in forest ecosystems. Trees 2, 571–578. http://dx.doi.org/10.1007/s00468-015-1308-y.
Ojanen, P., Minkkinen, K., Alm, J., Penttilä, T., 2010. Soil-atmosphere CO_2, CH_4 and N_2O fluxes in boreal forestry-drained peatlands. Forest Ecol. Manage. 260, 411–421.
Ostonen, I., Helmisaari, H.-S., Borken, W., Tedersoo, L., Kukumägi, M., Bahram, M., 2011. Fine root foraging strategies in Norway spruce forests across a European climate gradient. Glob. Change Biol. 17 (12), 3620–3632. http://dx.doi.org/10.1111/j.1365-2486.2011.02501.x.
Ostonen, I., Lõhmus, K., Pajuste, K., 2005. Fine root biomass, production and its proportion of NPP in a fertile middle-aged Norway spruce forest: comparison of soil core and ingrowth core methods. Forest Ecol. Manage. 212, 264–277. http://dx.doi.org/10.1016/j.foreco.2005.03.064.
Paal, J., 1998. Rare and threatened plant communities of Estonia. Biodivers. Conserv. 7, 1027–1049.
Peltoniemi, M., Mäkipää, R., Liski, J., Tamminen, P., 2004. Changes in soil carbon with stand age – an evaluation of a modelling method with empirical data. Glob. Change Biol. 10, 2078–2091. http://dx.doi.org/10.1111/j.1365-2486.2004.00881.x.
Peng, Y., Thomas, S.C., Tian, D., 2008. Forest management and soil respiration: implications for carbon sequestration. Environ. Rev. 16, 93–111.
Prescott, C., Godbold, D.L., Helmisaari, H.-S., Addo-Danso, S.D., 2016. Introduction to Forests, roots and soil carbon. Forest Ecol. Manage. 359, 321.
Repola, J., 2008. Biomass equations for birch in Finland. Silva Fennici 42 (4), 605–624.
Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., et al., 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562. http://dx.doi.org/10.1007/s004420000544.
Rytter, R.-M., 2013. The effect of limited availability of N and water on C allocation to fine roots and annual fine root turnover in *Alnus incana* and *Salix viminalis*. Tree Physiol. 33, 924–939. http://dx.doi.org/10.1093/treephys/tpt060.
Rytter, L., Rytter, R.-M., 2016. Growth and carbon capture of grey alder (*Alnus incana* (L.) Moench.) under north European conditions – Estimates based on reported research. Fores Ecol. Manage. 373, 56–65. http://dx.doi.org/10.1016/j.foreco.2016.04.034.
Salm, J.O., Kimmel, K., Uri, V., Mander, Ü., 2009. Global warming potential of drained and undrained peatlands in Estonia: a synthesis. Wetlands 29, 1081–1092. http://dx.doi.org/10.1672/08-206.1.
Saramäki, J., 1977. Development of white birch (*Betula pubescens* Ehrh.) stands on drained peatlands in Northern Central Finland. Commun. Instit. For. Fennici 91, 1–59 (in Finnish with English summary).
Schimel, D.S., House, J.I., Hibbard, K.A., Bousquet, P., Ciais, P., Peylin, P., et al., 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature 414, 169–172.
Silvola, J., Alm, J., Ahlholm, U., Nykänen, H., Martikainen, P.J., 1996. CO_2 fluxes from peat in boreal mires under varying temperature and moisture conditions. J. Ecol. 84, 219–228.
Simola, H., Pitkänen, A., Turunen, J., 2012. Carbon loss in drained forestry peatlands in Finland, estimated by re-sampling peatlands surveyed in the 1980s. Eur. J. Soil Sci. 63, 798–807.
Uri, V., Tullus, H., Lõhmus, K., 2002. Biomass production and nutrient accumulation in short-rotation grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural agricultural land. Forest Ecol. Manage. 161 (1–3), 169–179. http://dx.doi.org/10.1016/S0378-1127(01)00478-9.
Uri, V., Lõhmus, K., Ostonen, I., Tullus, H., Lastik, R., Vildo, M., 2007a. Biomass production, foliar and root characteristics and nutrient accumulation in young silver birch (*Betula pendula* Roth.) stand growing on abandoned agricultural land. Eur. J. For. Res. 126 (4), 495–506. http://dx.doi.org/10.1007/s10342-007-0171-9.
Uri, V., Vares, A., Tullus, H., Kanal, A., 2007b. Above-ground biomass production and nutrient accumulation in young stands of silver birch on abandoned agricultural land. Biomass Bioenerg. 31 (4), 195–204.
Uri, V., Lõhmus, K., Kiviste, A., Aosaar, J., 2009. The dynamics of biomass production in relation to foliar and root traits in a grey alder (Alnus incana (L.) Moench) plantation on abandoned agricultural land. Forestry 82(1), pp. 61–74, doi: http://dx.doi.org/10.1093/forestry/cpn040.
Uri, V., Lõhmus, K., Mander, Ü., Ostonen, I., Aosaar, J., Maddison, M., et al., 2011. Long-term effects on the nitrogen budget of a short-rotation grey alder (*Alnus incana* (L.) Moench) forest on abandoned agricultural land. Ecol. Eng. 37, 920–930. http://dx.doi.org/10.1016/j.ecoleng.2011.01.016.
Uri, V., Varik, M., Aosaar, J., Kanal, A., Kukumägi, M., Lõhmus, K., 2012. Biomass production and carbon sequestration in a fertile silver birch forest chronosequence. Forest Ecol. Manage. 267, 117–126. http://dx.doi.org/10.1016/j.foreco.2011.11.033.
Uri, V., Aosaar, J., Varik, M., Becker, H., Ligi, K., Padari, A., et al., 2014. The dynamics of biomass production, carbon and nitrogen accumulation in grey alder (*Alnus incana* (L.) Moench) chronosequence stands in Estonia. Forest Ecol. Manage. 327, 106–117. http://dx.doi.org/10.1016/j.foreco.2014.04.040.
Uri, V., Aosaar, J., Varik, M., Becker, H., Kukumägi, M., Ligi, K., et al., 2015. Biomass resource and environmental effects of Norway spruce (*Picea abies*) stump harvesting: An Estonian case study. Forest Ecol. Manage. 335, 207–215.
Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., Soosaar, K., et al., 2017. Carbon budgets in fertile grey alder (*Alnus incana* (L.) Moench.) stands of different ages. Forest Ecol. Manage. 396, 55–67. http://dx.doi.org/10.1016/foreco.2017.04.004.
Vanninen, P., Mäkelä, A., 1999. Fine root biomass of Scots pine stands differing in age and soil fertility in southern Finland. Tree Physiol. 19, 823–830. http://dx.doi.org/10.1093/treephys/19.12.823.
Varik, M., Aosaar, J., Ostonen, I., Lõhmus, K., Uri, V., 2013. Carbon and nitrogen accumulation in belowground tree biomass in a chronosequence of silver birch stands. Forest Ecol. Manage. 302, 62–70. http://dx.doi.org/10.1016/j.foreco.2013.03.033.
Varik, M., Kukumägi, M., Aosaar, J., Becker, H., Ostonen, I., Lõhmus, K., et al., 2015. Carbon budgets in fertile silver birch (*Betula pendula* Roth) chronosequence stands. Ecol. Eng. 77, 284–296. http://dx.doi.org/10.1016/j.ecoleng.2015.01.041.
Verlinden, M.S., Broeckx, L.S., Zona, D., Berhongaray, G., De Groote, T., Camino Serrano, M., et al., 2013. Net ecosystem production and carbon balance of an SRC poplar plantation during its first rotation. Biomass Bioenerg. 56, 412–422. http://dx.doi.org/10.1016/j.biombioe.2013.05.033.
Vogel, J.G., Gower, S.T., 1998. Carbon and nitrogen dynamics of boreal jack pine stands with and without of green alder understorey. Ecosystems 1, 386–400.
Vogt, K.A., Grier, C.C., Meier, C.E., Keyes, M.R., 1983. Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in Western Washington, as affected by fine-root input. Ecol. Monogr. 53 (2), 139–157. http://dx.doi.org/10.2307/1942492.
von Arnold, K., Nilsson, M., Hänell, B., Weslien, P., Klemedtsson, L., 2005a. Fluxes of CO_2, CH_4 and N_2O from drained organic soils in deciduous forests. Soil Biol. Biochem. 37 (6), 1059–1071. http://dx.doi.org/10.1016/j.soilbio.2004.11.004.
von Arnold, K., Weslien, P., Nilsson, M., Svensson, B.H., Klemedtsson, L., 2005b. Fluxes of CO_2, CH_4 and N_2O from drained coniferous forests on organic soils. Forest Ecol. Manage. 210, 239–254.
Walle, I.V., Van Camp, N., Van de Casteele, L., Verheyen, K., Lemeur, R., 2007. Short rotation forestry of birch maple, poplar and willow in Flanders (Belgium). I – biomass production after 4 years of tree growth. Biomass Bioenerg. 31, 267–275.
Waring, R.H., Running, S.W., 2007. Forest Ecosystems: Analysis at Multiple Scales. Academic Press, San Diego, pp. 263–291.
Whittaker, R.H., Woodwell, G.M., 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forests. Ecology 56 (1), 1–25.
WRB, 2006. World Reference Base for Soil Resources 2006, second ed. World Soil Resources Reports No. 103. FAO, Rome.
Wu, Z., Dijkstra, P., Koch, G.W., Peñuelas, J., Hungate, B.A., 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Glob. Change Biol. 17, 927–942. http://dx.doi.org/10.1111/j.1365-2486.2010.02302.x.
Wu, J., Larsen, K.S., van der Linden, L., Beier, C., Pilegaard, K., Ibrom, A., 2013. Synthesis on the carbon budget and cycling in a Danish, temperate deciduous forest. Agric. Forest Meteorol. 181, 94–107. http://dx.doi.org/10.1016/j.agrformet.2013.07.012.
Zhang, Q., Wang, C., Wang, X., Quan, X., 2009. Carbon concentration variability of 10 Chinese temperate tree species. Forest Ecol. Manage. 258 (5), 722–727. http://dx.doi.org/10.1016/j.foreco.2009.05.009.

Morozov, G., Aosaar, J., Varik, M., Becker, H., Aun, K., Lõhmus K.; Kukumägi, M., Uri, V. (20XX). The effect of thinning on annual net nitrogen mineralization and nitrogen leaching fluxes in silver birch and Scots pine stands. Submitted to Scandinavian Journal of Forest Research.

The effect of thinning on annual net nitrogen mineralization and nitrogen leaching fluxes in silver birch and Scots pine stands.

Gunnar Morozov[1 *], Jürgen Aosaar[1], Mats Varik[1], Hardo Becker[1], Kristiina Aun[1], Krista Lõhmus[2], Mai Kukumägi[2], Veiko Uri[1]

[1]Estonian University of Life Sciences, Institute of Forestry and Rural Engineering, Department of Silviculture, Kreutzwaldi 5, 51006 Tartu, Estonia

[2]University of Tartu, Institute of Ecology and Earth Sciences, Vanemuise 46, 51014 Tartu, Estonia

*Corresponding author: E-mail. Gunnar.morozov@emu.ee; tel: +37256689865

Submitted to Scandinavian Journal of Forest Research

The effect of thinning on annual net nitrogen mineralization and nitrogen leaching fluxes in silver birch and Scots pine stands

Highlights: Thinning effect on the annual NNM flux is site type and tree species specific; Nitrification increases in the silver birch stand, which also affects NNM flux positively; Thinning effect is of short term and lasts for the first post-thinning and disappears thereafter; The long term dynamics of annual NNM in silver birch stand is in decline; Thinning did not have any effect on NNM of Scots pine stand; Thinning does not induce more intensive N leaching.

Abstract

Thinning changes the functioning of the whole forest ecosystem, including carbon and nitrogen (N) cycling. The input of organic matter and N into soil, as well as soil temperature and moisture regimes changes, which may affect the intensity of the net nitrogen mineralization (NNM) process.

The main aim was to estimate the effect of thinning on annual NNM intensity in young silver birch (*Betula pendula* Roth.) and Scots pine (*Pinus sylvestris* L.) stands. Another aim of the study was to estimate the effect of thinning on annual N leaching.

Thinning increased annual NNM flux in silver birch stand. Nitrification increased, annual ammonification flux did not change. The effect of thinning was only revealed for the first post-thinning year and was lost thereafter. The 13-year dynamics of annual NNM in the birch stand revealed a significant decrease, which may be attributed to the effect of previous land use.

Annual NNM flux in Scots pine plots was practically the same; thinning did not affect N mineralization intensity. The effect of thinning on annual NNM flux was site and tree species specific.

Thinning did not induce more intensive N leaching. In the birch stand the effect of thinning on N leaching was reducing.

Keywords: *Betula pendula*, *Pinus sylvestris*, net nitrogen mineralization, thinning, nitrate, leaching

1 Introduction

Nitrogen (N) is one of the most important nutrient elements which affects the growth and production of forest trees in the boreal and hemiboreal regions. Generally, availability of N in forest ecosystems is limited and its low level inhibits the growth of trees. Although the total soil N pool can be even as large as 8-9 t ha^{-1} (Gundersen, 1995; Becker et al., 2015), the share of mineral N, which is available for the uptake by plants annually, forms only a small share (0.1–1%) of the total soil N pool (Helmisaari, 1995). Available mineral N is produced from organic matter by *in situ* mineralization (Tate, 1995) and net nitrogen mineralization (NNM) is one of the most important fluxes in the N cycle of boreal and temperate forests (Goodale and Aber, 2001; Lovett et al., 2002). NNM is affected by several factors, tree species and soil type being the most crucial among them (Tietema and Verstraten, 1992; Lovett et al., 2002; Uri et al., 2008). Moreover, the intensity of NNM depends on many abiotic environmental factors like soil temperature, moisture, pH, etc., but also land use history may play a role (Zak et al., 1990; Goodale and Aber, 2001; Lovett et al., 2002;

Becker et al., 2018). Although forest management evidently has some impact on NNM, the issue is still poorly studied and the results obtained pertain mainly to clear cutting (Kataja-aho et al., 2012) and stump harvesting (Becker et al., 2016). On the one hand, it is obvious that increased mineral N in soil enhances plant growth and forest productivity. On the other hand, the escalated NNM flux may lead to losses of N through leaching and gaseous emissions unless additional N is assimilated by trees or other vegetation (Piirainen et al., 2007).

Commercial thinning is one of the main silvicultural tools for moulding the species composition, quality and structure of future forest. Thinning is mainly carried out in stands of young to middle age and involves removal of commercial timber and letting the remaining trees of higher quality grow until final cutting. The main aim of commercial thinning is to mitigate competition between remaining trees and to increase the economic value of the whole stand through achieving better quality and higher annual radial increment of individual trees.

Usually, after thinning the remaining trees start to grow faster compared with the pre-thinning period, which is mainly caused by reduced competition and increased available nutrients and other resources (Mäkinen and Isomäki, 2004a). It has been found that thinning can redistribute available resources to enhance the vitality and increment of the retained trees (Mäkinen and Isomäki, 2004bc; Mäkinen et al., 2006). Moreover, thinning changes the functioning of the forest ecosystem a great deal, including carbon and nutrient cycling.

After thinning, the input of organic matter and N into soil, as well as soil temperature and moisture regime change, affecting the intensity of the NNM process one way or the other. Due to increased soil temperature more intensive NNM can be expected, which contributes to the increased production of trees. On the one hand, the reduced organic aboveground litter input in to soil may reduce annual NNM. On the other hand, the increased belowground litter input in to soil (fine root litter from cut trees) may increase the NNM. Despite the fact that thinning is widely used in forest management, studies dealing with impacts of commercial thinning on the soil inorganic N stock as well as on soil N fluxes are scarce. A study by Thibodeau et al. (2000) suggested a possible limiting effect of commercial thinning on annual NNM. Fang et al. (2016) found high intensity thinning to (30-50%) increase annual NNM significantly due to elevated soil temperature and moisture content, which is a direct result of a decrease in canopy closure. Thus annual NNM might be one factor which directly affects the production of forest during the post-thinning period, however, relevant data about this issue are scanty.

Silver birch (*Betula pendula* Roth.) and Scots pine (*Pinus sylvestris* L.) are two of the most common tree species along with Norway spruce (*Picea abies* (L.) Karst.) in northern temperate and boreal forests in Europe. In Estonia Scots pine makes up 35.3 % of the total growing stock and silver and downy birch combined occupy a second place with 26.1% (Yearbook 2017). Birch is commercially the most important source of hardwood in Northern and Eastern Europe, producing high-quality plywood, saw timber, pulpwood and firewood (Hynynen et al., 2010). Scots pine is ecologically and economically one of the most important tree species in Estonia, providing the timber industry with high quality raw material. Both species are light demanding, fast growing pioneer trees that are able to reforest land after clear-cutting and forest fires (Fischer et al., 2002;

Parro et al., 2015). Silver birch prefers fairly fertile well-drained sandy and silty till soils and fine sandy soils (Hynynen et al., 2010). Unlike silver birch, Scots pine is able to produce quality wood in different soils conditions of a wide range.

The main aim of the present study was to estimate the effect of thinning on annual NNM intensity in young aged silver birch and Scots pine stands. Since N loss from the ecosystem is related to annual NNM intensity, another aim of the study was to estimate the effect of thinning on annual N leaching.

We hypothesised that thinning will intensify annual NNM due to elevated soil temperature and annual N leaching will increase due to the increased concentration of mineral N in soil.

2 Materials and methods

2.1 Description of the study sites

For the study, a 20-year old silver birch stand (58°14′N; 26°44′E) and a 25-year old Scots pine stand (57°58′N; 27°20′E) in south-eastern Estonia were selected. In both study stands two sample plots were established in 2015; harvesting thinning was carried out at one plot and the other plot remained the control (Table 1). The selected silver birch stand had been thoroughly studied during a longer period (Uri et al., 2007; 2008; 2012; Varik et al., 2015; Aosaar et al., 2016) and the previous sample plot within this stand was considered the control plot. The thinned plot was established next to the existing plot. In the Scots pine stand both control and thinned plot were

established simultaneously. The intensity of thinning was 17% and 33% of the basal area of the stand for birch and pine, respectively. The dimensions of the established sample plots were 15x21m, in the silver birch stand, and 30x30m in the Scots pine stand. The main stand characteristics for the study sites were measured (Table 1). The silver birch stand was growing on former agricultural land and, according to historical records, the Scots pine stand had always been afforested.

[Table 1 near here]

In each sample plot (control and thinned), seven soil pits (depth 1.0 m) were dug in 2016; the soil profile was described and the soil type was determined according to the IUSS Working Group WRB (2006). Owing to the properties of the fertile site and fast decomposition of organic litter the forest floor was missing in the birch stand, and a thin layer of only 2-3 cm of well decomposed litter (O3) was found in the pine stand.

For estimation of the soil nitrogen (N) pool as well as the soil nutrient status, samples for chemical analyses from twelve random points over each sample plot were taken from the upper 0-10, 10-20 and 20-30 cm soil layers with a soil corer to form a composite sample (Table 2) (Uri et al., 2017ab). The content of soil nutrients and organic matter as well as soil pH were analysed in three replicates for each depth layer. For calculation of the total N storages in the soil, its bulk density was also determined. From every soil pit, bulk density samples were taken from the different soil mineral layers (0-30 cm) using a stainless steel cylinder (Ø 40 mm; V=50 cm^3), to avoid compression of

the soil and to preserve soil structure. In the laboratory, the samples were dried to constant weight at 105 °C and weighed.

[Table 2 near here]

2.2 Net nitrogen mineralization experiment

The NNM experiment was conducted by using the incubated polyethylene bags technique (Eno, 1960), which was used also in our earlier studies (Uri et al., 2003, 2008 and Becker et al., 2015; 2016; 2018). Thin polyethylene film ensured penetration of gases (O_2, CO_2, N_2, etc.), but the direct uptake of N by plants, as well as leaching and the additional input of soluble N into the bags were prevented. The experiment was carried out in the 10 cm topsoil layer and 24 samples were incubated both in the control and thinned plots. The samples were incubated randomly along the diagonal traversing the plot using a cylindrical corer (Ø 48 mm). The internal diameter of the corer was 1.6 mm larger than its cutting edge to avoid compression and mixing of the soil, which could have affected NNM significantly (Raison et al., 1987; Stenger et al., 1995; Persson and Wirén, 1995). Sampling and incubation were carried out at approximately a monthly interval, which is a conventional period allowing to observe changes in concentrations of the mineral forms of N (Adams et al., 1989); it has also been a standard period in previous similar studies (Uri et al., 2011; Becker et al., 2015, 2016, 2018). The samples were gathered by threes into composite samples and were transported to the laboratory on the same day. Simultaneously with the incubation of new samples, an initial sample was taken from the adjacent incubated sample each time.

The NNM experiment in the Scots pine and silver birch study sites was initiated in May 2016 and July 2016, respectively. The experiment was completed in the Scots pine stand and in the silver birch stand in April and October 2017, respectively. Although the experiment had been planned to last one year for both stands, we continued the study in the birch stand where a significant effect of thinning on annual NNM was found. And for clarifying further dynamics, the experiment was continued for one more year. For the pine stand, where the effect of thinning was not revealed, the experiment was completed.

The long-term dynamics of NNM in the silver birch stand during development of the forest ecosystem was demonstrated in our two previous NNM experiments carried out in the same site. The experiment in which we used the above described incubated polyethylene bags method took first place in 2004–2005 (Uri et al., 2008), and the second experiment lasted from May 2014 to May 2015.

2.3 Nitrogen leaching

Leaching of nitrogen (N) was estimated using stainless steel plate lysimeters (Roots and Voll, 2011; Uri et al., 2011; Becker et al., 2015). In all study areas, 14 stainless steel plate lysimeters were installed (7 for the thinned plot + 7 for the control plot) in the soil to a depth of 40 cm at random points of the plot. The collecting area of a lysimeter was 627 cm^2. The lysimeters were connected to water collectors (6000 ml polyethylene canisters disposed at a depth of 1 m) by means of polyethylene tubes. Water from the canisters was sampled, using a peristaltic vacuum pump, through a plastic pipe. Water was sampled monthly from early spring to late autumn (up to the

freezing of the soil). The leaching flux of N was calculated separately for every sampled month on the basis of the amounts of percolated water (sum of 7 lysimeters), taking into account the N concentrations analysed from the water samples. The annual cumulative leaching flux was calculated by summing up the amounts of leached N for the different months.

2.4 Chemical analysis

Tecator ASN 3313 was employed for testing the soil samples for nitrogen after Kjeldahl. The concentration of $N\text{-}NO_2$, $N\text{-}NO_3$, and $N\text{-}\ NH_4$ + in the soil was determined by flow injection analysis with Tecator ASN 65-32/84 and Tecator ASN 65- 31/84. Nitrite (NO2-N) nitrogen concentration was only analysed from the first sampling and since the concentration of nitrite N was negligible it was excluded from further analyses. Soil pH was determined in a 2.5:1 KCl soil (vol/wt) suspension. Available phosphorus was determined by flow injection analysis with the use of Tecator ASTN 9/84 and the content of available potassium was determined from the same solution by the flame photometric method. Soil magnesium content was determined by flow injection analysis with Tecator ASTN 90/92 and calcium content was determined from the same solution by the flame photometric method. The water samples were analysed for NH4, NO2, NO3 at the Biochemistry Laboratory of the Estonian University of Life Sciences and dissolved organic nitrogen (DON) was analysed at the Laboratory of the Estonian Environmental Research Ltd, using standard methods for water research (APHA, 1989).

2.5 Statistics

Normality of variables was checked using Lilliefors and Shapiro-Wilk's tests. To analyse the effect of the treatment factor (harvesting thinning) on the response variables, ANOVA was applied. The ANOVA assumptions - normality, homogeneity of group variances and nonsignificant relationship between the group means and the standard deviations - were checked. For multiple comparisons of the means, in case the assumptions were satisfied, the t-test was employed to compare the two group means. The Wilcoxon Matched Pairs test was used to test the significance of NNM intensity for the different treatments and Welsh t-test was used to test the significance of N content for the different treatments. The Spearman Rank Correlation was used to analyse the relationship between annual NNM intensity and soil temperature. In all cases the level of significance 0.05 was accepted.

3 Results

3.1 Mineral nitrogen content dynamics in soil

Silver birch

During the first year after thinning (2016) the content of soil mineral N fluctuated monthly in the thinned plot; in the control plot its content across the studied months was more stable (Fig. 1). However, the share of mineral N for the upper 10 cm soil layer in the control and thinned plots was quite low, varying between 1.9 and 4.0 mg kg^{-1} and between 1.7 and 5.7 mg kg^{-1}, respectively. Average soil mineral N content was higher in the thinned plot, showing a statistically significant difference ($P<0.05$) for four months (Fig. 1). Soil mineral N content was substantially higher at a younger stand age (8 years), varying between 26.7 and 35.5 mg kg^{-1} (Uri et al., 2008). Thereafter it started to decrease and was at the same level in 2014 (0.14 and 2.62 mg kg^{-1}) as in 2016-2017.

Soil mineral N content peaked both in the control and thinned plots in April 2017, being 4.0 and 5.7 mg kg^{-1}, respectively. During the second post-thinning vegetation period (2017) it decreased steadily and was at its lowest in August. When in the first post-thinning year (2016) soil mineral N content in the thinned plot fluctuated from month to month, then in 2017 its values were more stable. However, although the relative change of mineral N content between the studied months was marked, then its absolute values changed only 2-3 mg kg^{-1}. Regarding the different forms of mineral N, ammonium N (NH^{+}_{4}) was the dominating in the soil, making up 83.2% to 100% and 59.9 to 100% of total mineral N in the control and thinning plots during the whole study period, respectively.

[Figure 1 near here]

The average soil ammonium N content was slightly higher in the control plot, but this difference did not reach statistical significance (P=0.84, Welsh t-test). However, the average concentration of nitrate N revealed a statistically significant difference (P<0.05); the average concentration of NO^{-}_{3} in the soil of the thinned plot was higher throughout the study period (Appendix 2).

Scots pine

The annual dynamics of the soil mineral N content in the Scots pine stand was quite similar in both the thinned and control plots. For the study period from May to November 2016, the monthly values of mineral N were generally low and varied between 1.1 to 3.3 mg kg^{-1} at the control plot, and from 1.5 to 3.5 mg kg^{-1} at the thinned plot (Fig. 2). Soil mineral N content differed significantly between

the study variants only in November. The dominating form of soil mineral N in both study plots was ammonium nitrogen (NH^{+}_{4}) making up roughly 100% (99.7-99.9%) of the total soil mineral N content.

[Figure 2 near here]

3.2 Dynamics of annual net nitrogen mineralization

Silver birch

The dynamics of the net nitrogen mineralization (NNM) flux in the silver birch stand over the whole study period (2016 - 2017) was different in the control and thinned plots (Fig. 3). However, the difference was larger in the first year after thinning (2016), which levelled out in the following year (2017). In most cases monthly NNM was higher in the thinned plot, being significantly higher during the three studied months (Fig. 3). Thinning was a significant factor which affected the annual NNM flux during the first post-thinning year (ANOVA, $F=17.1$; $P<0.001$). Thinning increased the total annual NNM flux which was 24 kg ha^{-1} higher in the thinned plot. When the annual flux of ammonification was practically similar in the control and thinned plots, then the nitrification flux was almost threefold higher in the thinned plot (Table 3).

NNM intensity peaked in late summer (August-September) in the thinned plot while its monthly fluctuation was much lower and smoother in the control plot (Fig. 3). The average intensity of

nitrification was significantly higher ($P<0.05$) in the thinned plot (41.7 versus 113.0 mg kg^{-1} N day^{-1}). The dynamics of annual ammonification was similar in both study plots ($P=0.49$).

The first NNM experiment in this silver birch stand was carried out in 2004-2005 (Uri et al., 2008) and a repeat NNM experiment was performed from April 2014 to May 2015 with the use of the described polyethylene bags method. The 13-year period of stand development (from 2004 to 2017) revealed a decrease of the annual NNM flux: when in the young stage the annual NNM flux was 99 kg ha^{-1} yr^{-1} for the upper 10 cm soil layer (Uri et al., 2008), then ten years later (2014-2015) it was only 52 kg ha^{-1} yr^{-1}. In the current study (2016-2017) the NNM flux in the control plot was estimated at only 30 kg ha^{-1} yr^{-1} (Table 3).

[Figure 3 near here]

There was a strong correlation between soil temperature and NNM intensity (mg kg^{-1} N day^{-1}) during the first post-thinning year (2016) both in the control plot ($r= 0.90$) and in the thinned plot ($r=0.88$) (Spearman Rank Correlation). However, in the following study year (2017) this relationship was obliterated (Fig. 3). A significant relationship between monthly NNM intensity and soil moisture content ($P>0.05$) in the control or thinned plot was not proven.

Scots pine

In the studied Scots pine stand the dynamics of annual NNM intensity was similar between the control and thinned plots (Fig. 4) (ANOVA, F=1.09; P=0.30), i.e. there was not significant effect of thinning on NNM. Since there was practically no difference in NNM intensity between the thinned and the control plot during the first post-thinning year, the length of the experiment was limited to one year.

[Figure 4 near here]

The nitrification process in the soil was almost absent and ammonification practically made up total annual NNM (Table 3). Like in the silver birch stand, the intensity of NNM depended significantly on soil temperature both in the control and thinned plots (r=0.86 and r=0.82, respectively) (Spearman Rank Correlation).

[Table 3 near here]

3.3 Environmental factors

Silver birch

Thinning affected soil volumetric moisture content, which was significantly lower in the thinned plot during almost all studied months, except for spring 2017 (Appendix 1). The dynamics of soil temperature was practically similar in the thinned and control plots (Fig. 3) except for only one

month in mid-summer 2017 when average soil temperature was significantly higher in the thinned plot (Appendix 1).

Generally, the dynamics of soil pH followed the same pattern in the control and thinned plots (Fig. 5). However, at the end of the vegetation period 2016 there was a significant difference in soil pH between the control plot and the thinned plot (Fig 5). The long term dynamics of soil pH in upper 0-10 cm soil layer demonstrated a slight decrease; when in 2004 average soil pH was 5.60, then in 2014 it was 5.47; in 2016-2017 soil pH was 5.38 in the control plot and 5.43 in the thinned plot.

[Figure 5 near here]

Scots pine

In the Scots pine stand soil temperature in the thinned plot and in the control plot was significantly different almost during the whole study period, with the exception of autumn 2016 (Appendix 1). In the warmer period (May-Aug.) soil temperature was higher (0.9-1.3°C) in the thinned plot than in the control plot, however, in the cold period (Dec.-March) soil temperature was lower (0.7-0.9°C) in the thinned plot compared to the control plot. Soil moisture was significantly higher (4.6-14.1%) in the thinned plot than in the control plot during the whole study period ($p<0.05$) (Appendix 1).

[Figure 6 near here]

The annual dynamics of soil pH was different for the thinned and control plot. Soil pH was significantly higher in the thinned plot in the June-August of the first post-thinning year and in the April-May 2017; the pH in the thinned plot decreased in autumn of 2016 (Fig. 6).

3.4 Nitrogen leaching

Silver birch

The annual flux of N leaching was generally low, but it was higher in the control plot than in the thinned plot, 5.5 versus 2.3 kg N ha^{-1} yr^{-1}, respectively. Also the amount of percolated water demonstrated a different pattern for the two plots, 2100 t ha^{-1} yr^{-1} for the control plot and 930 t ha^{-1} yr^{-1} for the thinned plot.

Nitrate nitrogen (NO_3-N) and organic dissolved N (DON) made up most of leached N (Fig. 7). Nitrate (NO^-_3) made up 39% of all leached N in the control plot and 45% in the thinned plot. The share of DON in leached soil water was 57% in the control plot and 52% in the thinned plot. The share of ammonium N was relatively low, accounting for 4% and 3% of total leached N in the control plot and in the thinned plot, respectively. In both variants N leaching peaked in early spring (April).

[Figure 7 near here]

Scots pine

In the Scots pine stand the amount of percolated water was practically negligible. Although all lysimeters were sampled monthly, water was found in the collectors only in a few cases. The amount of leached N in the percolated soil water of the Scots pine stand was 43.4 g N ha^{-1} yr^{-1} in the control plot and 142.8 g N ha^{-1} yr^{-1} in the thinned plot.

The amount of percolated soil water was 40 t ha^{-1} yr^{-1} in the control plot and 80 t ha^{-1} yr^{-1} in the thinned plot. Most of leached N was made up by ammonium N and DON. In the control plot the share of ammonium N was 49% and the share of DON was 50% of annual leached soil water. In the thinned plot, the respective shares were 36% and 57%. Nitrate N was almost missing, with one exception in a sample from the thinning plot in August 2016 (Fig. 8.). The share of NO^{-}_{3} in the control and thinning plots was 1% and 6%, respectively.

[Figure 8 near here]

4 Discussion

Commercial thinning is a widely used silvicultural method for improving growth conditions for remaining trees as well as for enhancing the economic value of future stands. Thinning intensifies the production of remaining trees, including stem diameter increment, which in some cases allows to reduce the rotation length of stands. Thinning also improves stand quality, which is an important issue for some tree species, e.g silver birch. Some authors (Zhou et al., 2016) have found thinning

to be beneficial also regarding other aspects: increase in understorey diversity and biomass and improvement in soil properties, nutrient cycling and soil water content. To offset the advantages, commercial thinning has been found to negatively affect wood quality as a result of infection by *Heterobasidion* spp in conifer stands e.g. Norway spruce (Gunulf et al., 2013; Ronnberg et al., 2013; Gaitnieks et al., 2018). Speaking about the accompanying environmental effects of thinning on ecosystem's functioning, a possible impact on nitrogen (N) cycling should be considered, since availability of N among the crucial factors limiting tree growth and photosynthetic capacity in boreal forests (Luo et al., 2004).

In the current study the effect of thinning on the annual NNM flux demonstrated different patterns in the studied deciduous and conifer stands; the effect was evident for the silver birch stand but not for the Scots pine stand (Table 3).

Silver birch

In the birch stand the total soil N pool in the upper 10 cm layer was similar in the control plot and in the thinned plot (roughly 1.4 t N ha^{-1}) (Table 2). The total N pool in the 0-30 cm soil layer varied between 3.5 and 3.8 t N ha^{-1}, which remains in the range of the total N pool for boreal forest ecosystems, and was as a rule 1–8 t ha^{-1} (Gundersen, 1995). In boreal forest soils, most of N is bound within soil organic material while only a small amount (about 0.1–1%) is available to plants in the inorganic form (Helmisaari, 1995). In the current study the share of mineral N was higher, accounting for 2.2–3.7% of the soil N pool in the upper 0–10 cm soil over the longer study period (2004-2017).

In the studied stand soil mineral N content decreased in the course of stand development: when in the 8-year–old stand (2004) the measured nitrate N content in 10 cm topsoil varied between 24 and 35 mg kg^{-1} (Uri et al., 2008), then in 2016-2017 it was only 1.7-5.7 mg kg^{-1}. Ammonium nitrogen was the main form of mineral N in the soil both in the control and thinned plots, however, soil nitrate N content was very low in both plots. The lower soil mineral N content can be attributed to decreased net nitrification intensity (Table 3) which value was roughly threefold lower compared with that for the 8-year-old stand (2004). Of course, the content of mineral N depended on NNM intensity on the one hand and on the uptake by plants on the other hand. In a 10-year-old birch stand the total annual N demand of plants was 118 kg ha^{-1} yr^{-1} (Aosaar et al., 2016) and the largest share of annual N demand (60%) was expended for the production of leaves. The foliage mass in broadleaved stands usually reaches a stable level (3-4 t ha^{-1}) at the age of 10 years. Thus we can assume that the magnitude of the annual N demand of plants did not change and the decrease of mineral N in the studied stand was mainly induced by the reduced annual NNM flux.

The dynamics of soil mineral N content was affected by thinning: in the thinned plot mineral N fluctuated monthly during the first post-thinning year while in the control plot its content demonstrated a relatively smooth course (Fig. 1). The lowest mineral N content was recorded in late autumn for both study plots, which can be explained by low soil temperature and decreased NNM.

Soil temperature is among of the crucial factors influencing the N mineralization process in the soil (Tietema and Verstraten, 1992). Relationship between NNM and soil temperature has been found in several studies (Powers, 1990; Tietema and Verstraten, 1992; Goncalves and Carlyle, 1994; Uri et al., 2003; Becker et al., 2015). In our study the monthly intensity of NNM followed the dynamics of soil temperature during the first post-thinning year (Fig. 3) which is in good accordance with above referred results. However, during second post thinning year no correlation was found between soil temperature and NNM intensity, which is difficult to explain. Evidently, meteorological conditions may have played a role in this case (precipitation in 2017 was higher than usual).

In the control plot the dynamics of annual NNM followed a quite characteristic trend, i.e. NNM was more intensive in spring or early summer and in autumn (Fig. 3), which can be mainly explained by the input of decomposable fresh organic matter to the soil via litter. According to Nadelhoffer et al. (1984), mineralization intensity is the highest in spring or early summer (May, June) while another peak occurs at the end of the vegetation period (August, September). Two peaks of annual NNM for grey alder stands of the same age, growing on similar soils on abandoned agricultural land in Estonia, were also found: a spring peak in May and a less pronounced autumn maximum in September (Uri et al., 2003).

Thinning significantly intensified net nitrification whereas ammonification remained at the same level during the first post-thinning year; the annual cumulative NNM flux was roughly two times as high in the thinned plot as in the control plot, 30 and 54 kg ha^{-1} yr^{-1}, respectively (Table 3). In

the second year after thinning this difference was levelled out (Fig. 3) and although NNM in the thinned plot was higher in almost all study periods, a statistically significant difference was only found for one study month (July-August). Thus, effect of the thinning on NNM intensity was of short duration, being limited to one post-thinning year.

Owing to the fact that the silver birch stand had a long study history (Uri et al., 2007, 2008), the decrease of annual NNM became apparent. In the 8-9 year-old stand (2004-2005) the annual NNM flux was roughly 100 kg ha^{-1} yr^{-1} estimated for the upper 10 cm soil layer (Table 3). Ten years later (2014-2015) it was almost two times as low (roughly 50 kg ha^{-1} yr^{-1}) and in the 21-year old stand it was only 30 kg ha^{-1} yr^{-1} (Table 3, control plot). This can probably indicate a decline of the effect of land use history; birch stand had emerged on a former agricultural land. The more intensive NNM in this stand has been induced by the trees in an earlier developmental phase compared with the adjacent non-forested grassland (Uri et al., 2008). Thereafter annual NNM started to decrease; however, it was nitrification intensity that decreased while the rate of ammonification remained almost the same. Some studies support the standpoint that potential N mineralization and nitrification in forested old fields are the highest in the early forest succession period (Thorne and Hamburg, 1985). Some researchers found an increase in NNM, especially nitrification, with an increasing stand age (Zak et al., 1990; Robertson and Vitousek, 1981). Also the share of nitrification of total NNM varied during stand development: when in the 8-year-old stand (2004) nitrification made up ca 60% of total NNM, then ten years later it made up more than 70% and in the 21-year old stand it had decreased to around 50%. Thinning affected this share, for in our study it was around 70% of total soil NNM (Table 3).

Since decreased NNM means a smaller amount of available N for plant's annual uptake, there may arise the question about covering the plant's annual N demand. Although we only considered the NNM flux from in the upper 0-10 cm soil layer, the subsequent soil layer (10-20 cm) could also significantly contribute to covering the N demand of plants. As we demonstrated in our earlier study (Uri et al., 2008), the annual NNM flux in the 10-20 cm soil layer accounted for up to 37% of total soil NNM. Still, the most active part of the forest soil is the topsoil where most of the fine roots, nutrients and microbial biomass are accumulated (Lõhmus et al., 2006; Varik et al., 2013).

The leaching of N in the silver birch stand was modest in magnitude. In the control plot it was even larger (5.5 kg ha^{-1} yr^{-1}) than estimated for the 10-year-old stand (ca 1 kg N ha^{-1} yr^{-1}) (Aosaar et al., 2016). Nitrogen leaching may vary to a large extent for different years, depending mostly on annual precipitation as well as N transformation processes in soil. The effect of thinning on annual N leaching was contrary to our expectations. Usually, thinning should increase both the amount of percolated water and nutrient release as a consequent of decreased canopy closure and increased precipitation onto forest ground, as well as a consequence of the additional input of organic matter to soil from fine root necromass and residues. In this study, annual N leaching in the thinned plot was smaller due to a lesser amount of percolated water. The only rational explanation for this phenomenon would be more intensive growth of the herbaceous understorey in the thinned area. Because of favourable light conditions in the thinned plot, the growth of the herbaceous understorey intensified greatly, which prevented precipitation reaching the soil and contributed to quicker uptake of water by plants.

Scots pine

Although NNM intensity in the pine stand for the studied months was slightly higher in the thinned plot (Fig. 4), the difference between the control plot and the thinned plot was insignificant. Thus the effect of thinning on NNM intensity was not found; the total annual NNM flux was virtually equal in the thinned and control plots (Table 3). Its value of roughly 20 kg ha^{-1} yr^{-1} (Table 3) is in accordance with the results of similar Estonian studies where it varies between 6 and 30 kg N ha^{-1} yr^{-1} in conifer stands (Pajuste and Frey, 2003; Külla et al., 2004). NNM intensity in both the thinned and control plots in October-November was negative, which indicates microbial N immobilization in the soil (Fig. 4). Higher soil temperature in the thinned plot during the vegetation period as well as increased soil moisture in the dry sandy soil may have resulted in more intensive NNM.

The dominating N mineralization process was ammonification, which is typical for poor and acid sandy soils. Usually, a low pH level and a high CN ratio are inherent in pine stands, which was also the case in this study (Table 2). Although the range of pH values for nitrification is quite wide, e.g. from 3.9 up to 6.3 (Van Praag and Weissen, 1973), it usually fell below 4.0. According to Persson and Wirén (1995), low pH often inhibits nitrification so that almost no nitrification can be detected at pH_{H2O} <4. In the studied pine stand soil pH was 3.8, which is below the lower limit of nitrification threshold. Normally, nitrification increases with a decreasing C:N ratio (Vervaet et al., 2002) and the threshold values for nitrification are about 22–24 (Lovett et al., 2004; Ollinger et al., 2002).

N leaching was practically negligible in both plots, which was caused by the small amount of percolated water and also by the low N concentration in sampled water. In leached water, ammonium N and organic N were the main forms of N while nitrate was almost missing, which is consistent with the NNM results: as the share of ammonification of total NNM was almost 100%, NH_4 was present in leached water as well as in the soil (Table 3, Fig. 2).

Conclusions

The effect of thinning on the annual NNM flux was site type and tree species specific. In the silver birch stand thinning increased the annual NNM flux through increased nitrification. However, this effect was of short term and was only revealed for the first post-thinning year and disappeared thereafter. The long term dynamics of annual NNM in silver birch stand demonstrated a significant decrease, which may indicate declining effect of land use history.

In the pine stand the annual NNM flux in the thinned and control plots was practically equal; the annual cumulative NNM flux in the thinned plot and in the control plot was similar, 19.4 and 20.3 kg N ha^{-1} yr^{-1}, respectively.

Annual N leaching was small in the birch stand and virtually negligible in the pine stand. Thinning did not induce more intensive N leaching, moreover, in the birch stand N leaching was even smaller compared with the control plot.

References

Adams MA, Polglase PJ, Attiwill MP, Weston CJ. 1989. In situ studies on nitrogen mineralization and uptake in forest soils: some comments on methodology. Soil Biol. Biochem. 21(39): 423–429.

Aosaar J, Mander Ü, Varik M, Becker H, Morozov G, Maddison M, Uri V. 2016. Biomass production and nitrogen balance of naturally afforested silver birch (Betula pendula Roth.) stand in Estonia. Silva Fenn. vol. 50(4): 1-19.

Becker H, Aosaar J, Varik M, Morozov G, Aun K, Mander Ü, Soosaar K, Uri V. 2018. Annual net nitrogen mineralization and litter flux in well-drained downy birch, Norway spruce and Scots pine forest ecosystems. Silva Fenn. vol. 52(4): 1-18.

Becker H, Aosaar J, Varik M, Morozov G, Kanal A, Uri V. 2016. The effect of Norway spruce stump harvesting on net nitrogen mineralization and nutrient leaching. For. Ecol. Manag. 377: 150–160.

Becker H, Uri V, Aosaar J, Varik M, Mander Ü, Soosaar K, Hansen R, Teemusk A, Morozov G, Kutti S, Lõhmus K. 2015. The effects of clear-cut on net nitrogen mineralization and nitrogen losses in a grey alder stand. Ecol. Eng. 85: 237–246.

Eno CF. 1960. Nitrate production in the field by incubating the soil in polyethylene bags. In: Proceedings of the Soil Science Society of America 24(4): 277–279.

Fang S, Lin D, Tian Y, Hong S. 2016. Thinning Intensity Affects Soil-Atmosphere Fluxes of Greenhouse Gases and Soil Nitrogen Mineralization in a Lowland Poplar Plantation. Forests 7(7): 141.

Fischer A, Lindner M, Abs C, Lasch P. 2002. Vegetation dynamics in central European forest ecosystems (near-natural as well as managed) after storm events. Folia Geobot. 37(1): 17 – 32.

Gaitnieks T, Brauners I, Kenigsvalde K, Zaļuma A, Brūna L, Jansons J, Burņeviča N, Lazdiņš A, Vasaitis R. 2018. Infection of pre-commercially cut stumps of Picea abies and Pinus sylvestris by Heterobasidion spp. – a comparative study. Silva Fenn. 52(1): 1-7.

Goncalves JLM, Carlyle JC. 1994. Modeling the influence of moisture and temperature on net nitrogen mineralization in a forested sandy soil. Soil Biol. Biochem. 26(11): 1557–1564.

Goodale CL, Aber JD. 2001. The long term effects of land-use history on nitrogen cycling in northern hardwood forests. Ecol. Appl. 11(1): 253–267.

Gundersen P. 1995. Nitrogen deposition and leaching in European forests - preliminary results from a data compilation. Water Air Soil Poll. 85(3): 1179-1184.

Gunulf A, Wang L, Englund J-E, Rönnberg J. 2013. Secondary spread of Heterobasidion parviporum from small Norway spruce stumps to adjacent trees. For. Ecol. Manag. 287: 1-8.

Helmisaari H-S, 1995. Nutrient cycling in Pinus sybestris stands in eastern Finland. Plant Soil 168-169(1): 327-336.

Hynynen J, Niemistö P, Viherä-Aarnio A, Brunner A, Hein S, Velling P. 2010. Silviculture of birch (Betula pendula Roth and Betula pubescens Ehrh.) in northern Europe. Forestry 83(1): 103–119.

Kataja-aho S, Samolander A, Fritze H, Norrgård S, Haimi J. 2012. Responses of soil carbon and nitrogen to stump removal. Silva Fenn. 46(2), 169–179.

Külla T, Lõhmus K, Kurvits V, Seemen H. 2004. In situ net nitrogen mineralisation in the organic layer under a middle-aged Rhodococcum Scots pine (Pinus sylvestris (L.) stand on podzol. Forestry Studies 40: 176–186.

Lõhmus K, Truu M, Truu J, Ostonen I, Kaar E, Vares A, Uri V, Alama S, Kanal A. 2006. Functional diversity of culturable bacterial communities in the rhizosphere in relation to fine-root and soil parameters in alder stands on forest, abandoned agricultural, and oil-shale areas. Plant Soil 283(1): 1–10.

Lõhmus E. 1984. Eesti metsakasvukohatüübid. Eesti NSV Metsamajanduse ja Looduskaitse Ministeerium, Eesti NSV Agrotööstuskoondise Info- ja Juurutusvalitsus, Tallinn, 76pp (in Estonian).

Lovett GM, Weathers KC, Arthur MA. 2002. Control of nitrogen loss from forested watersheds by soil carbon:nitrogen ratio and tree species composition. Ecosystems 5(7): 712–718.

Lovett GM, Weathers KC, Arthur MA, Schultz JC. 2004. Nitrogen cycling in a northern hardwood forest: do species matter? Biochem. 67(3): 289–308.

Luo Y, Su B, Currie WS, Dukes JS, Finzi AC, Hartwig U, Hungate B, McMurtrie RE, Oren R, Parton WJ, Pataki, DE, Shaw MR, Zak DR, Field CB. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. BioScience. 54(8): 731–739.

Mäkinen H, Isomäki A, Hongisto T. 2006. Effect of half-systematic and systematic thinning on the increment of Scots pine and Norway spruce in Finland. Forestry 79(1): 103-121.

Mäkinen H, Isomäki A. 2004a. Thinning intensity and growth of Norway spruce stands in Finland. Forestry 77(4): 349–364.

Mäkinen H, Isomäki A. 2004b. Thinning intensity and long-term changes in increment and stem form of Norway spruce trees. For. Ecol. Manag. 201(2): 295–309.

Mäkinen H, Isomäki A. 2004c. Thinning intensity and long-term changes in increment and stem form of Scots pine trees. For. Ecol. Manag. 203(1): 21–34.

Millard P, Sommerkorn M, Grelet GA. 2007. Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal. New Phytol. 175(1): 11-28.

Nadelhoffer KJ, Aber JD, Melillo JM. 1984. Seasonal patterns of ammonium and nitrate uptake in nine temperate forest ecosystems. Plant Soil 80(3): 321–335.

Ollinger SV, Smith ML, Martin ME, Hallett RA, Goodale CL, Aber JD. 2002. Regional variation in foliar chemistry and N cycling among forests of diverse history and composition. Ecology 83(2): 339–355.

Pajuste K, Frey J. 2003. Nitrogen mineralisation in podzol soils under boreal Scots pine and Norway spruce stands. Plant Soil 257(1): 237–247.

Parro K, Metslaid M, Renel G, Sims A, Stanturf JA, Jõgiste K, Köster K. 2015. Impact of postfire management on forest regeneration in a managed hemiboreal forest, Estonia. Can. J. For. Res. 45(9): 1192-1197.

Persson T, Wirén A. 1995. Nitrogen mineralization and potential nitrification at different depths in acid forest soils. Plant Soil 168-169(1): 55–65.

Piirainen S, Finér L, Mannerkoski H, Starr M. 2007. Carbon, nitrogen and phorphorus leaching after site preparation at a boreal forest clear-cut area. For. Ecol. Manag. 243(1): 10–18.

Powers RF. 1990. Nitrogen mineralization along an altitudinal gradient: interactions of soil moisture and substrate quality. For. Ecol. Manag. 30(1): 19–29.

Raison RJ, Conell MJ, Khanna PK. 1987. Methodology for studying fluxes of soil mineral N in situ. Soil Biol. Biochem. 19(5): 521–530.

Robertson GP, Vitousek PM. 1981. Nitrification potentials in primary and secondary succession. Ecology 62(2): 376-386.

Rönnberg J, Berglund M, Johansson U, Cleary M. 2013. Incidence of Heterobasidion spp. following different thinning regimes in Norway spruce in southern Sweden. Forest Ecol. Manag., 289: 409–415.

Roots OO, Voll M. 2011. New equipment for the collection of water percolating through the soil and bulk materials. Russ. J. Gen. Chem. 81(13): 2672–2675.

Stenger R, Priesack E, Beese F. 1995. Rates of net nitrogen mineralization in disturbed and undisturbed soils. Plant Soil 171(2): 323–332.

Tate RL. 1995. Soil microbiology. John Wiley & Sons, Inc, New York. 398 pp.

Thibodeau L, Raymond P, Camiré C, Munson AD. 2000. Impact of precommercial thinning in balsam fir stands on soil nitrogen dynamics, microbial biomass, decomposition, and foliar nutrition. Can. J. For. Res. 30(2): 229–238.

Thorne JF, Hamburg SP. 1985. Nitrification potentials of an old-field chronosequence in Campton, New Hampshire. Ecology 66(4): 1333–1338.

Tietema A, Verstraten JM. 1992. Nitrate cycling in an acid forest ecosystem in the Netherlands under increased atmospheric nitrogen input. Biogeochemistry 15(1): 21–46.

Uri V, Lõhmus K, Kund M, Tullus H. 2008. The effect of land use on net nitrogen mineralization on abandoned agricultural land: silver birch stand versus grassland. Forest Ecol. Manag. 255(1): 226–233.

Uri V, Lõhmus K, Mander Ü, Ostonen I, Aosaar J, Maddisson M, Helmisaari HS, Augustin J. 2011. Long-term effects on nitrogen budget of a short-rotation grey alder (Alnus incana (L.) Moench) forest in abandoned agricultural land. Ecol. Eng. 37(6): 920–930.

Uri V, Lõhmus K, Tullus H. 2003. Annual net nitrogen mineralization in a grey alder (Alnus incana (L.) Moench) plantation on abandoned agricultural land. Forest Ecol. Manag. 184(1–3): 167–176.

Uri V, Kukumägi M, Aosaar J, Varik M, Becker H, Soosaar K, Morozov G, Ligi K, Padari A, Ostonen I, Karoles K. Carbon budgets in fertile grey alder (Alnus incana (L.) Moench.) stands of different ages. Forest Ecol. Manag. 396: 55–67.

Uri V, Kukumägi M, Aosaar J, Varik M, Becker H, Morozov G, Karoles K. 2017b. Ecosystems carbon budgets of differently aged downy birch stands growing on well-drained peatlands. Forest Ecol. Manag. 399: 82–93.

Uri V, Varik M, Aosaar J, Kanal A, Kukumägi M, Lõhmus K. 2012. Biomass production and carbon sequestration in a fertile silver birch forest chronosequence. Forest Ecol. Manag. 267: 112–126.

Van Praag HJ, Weissen F. 1973. Elements of a functional definition of oligotrophic humus based on the nitrogen nutrition of forest stands. J. Appl. Ecol. 10(2): 569–583.

Varik M, Aosaar J, Ostonen I, Lõhmus K, Uri V. 2013. Carbon and nitrogen accumulation in belowground tree biomass in a chronosequence of silver birch stands. Forest Ecol. Manag. 302: 62–70.

Varik M, Kukumagi M, Aosaar J, Becker H, Ostonen I, Lohmus K, Uri V. 2015. Carbon budgets in fertile silver birch (Betula pendula Roth) chronosequence stands. Ecol. Eng. 77: 284–296.

Vervaet H, Massart B, Boeckx P, Van Cleemput O, Hofman G. 2002. Use of principal component analysis to assess factors controlling net N mineralization in deciduous and coniferous forest soils. Biol. Fertil. Soils 36(2), 93–101.

WRB. 2006. World Reference Base for Soil Resources 2006, second ed. World Soil Resources Reports No. 103. FAO, Rome. 145 pp.

Yearbook Forest 2017. Compiled by Estonian Environmental Information Centre. Tartu 2018. (In Estonian). [accessed 2018 Dec 06].

Zak DR, Grigal DR, Gleeson S, Tilman D. 1990. Carbon and nitrogen cycling during old-field succession: constraints on plant and microbial biomass. Biochemistry 11(2): 111–129.

Zhou L, Cai L, He Z, Wang R, Wu P, Ma X. 2016. Thinning increases understory diversity and biomass, and improves soil properties without decreasing growth of Chinese fir in southern China. Environ. Sci. Pollut. Res. 23(23): 24135–24150.

Table 1. Characteristics of the study sites in 2016; $D_{1,3}$ – average stand diameter at breast height, H – average stand height, G – basal area of stand, N – stand density, Site type – according to the Estonian classification (Lõhmus, 1984).

		Area of stand	$D_{1,3}$ (cm)	H (m)	G (m^2 ha^{-1})	N (trees ha^{-1})	Site type
Silver birch	control	9.8 ha	11.0	18.2	24.5	2600	*Oxalis*
	thinned		11.9	20.3	20.3	1840	
Scots pine	control	8.7 ha	11.1	13.9	26.5	2733	*Oxalis-Myrtillus*
	thinned		13.9	13.9	17.7	1178	

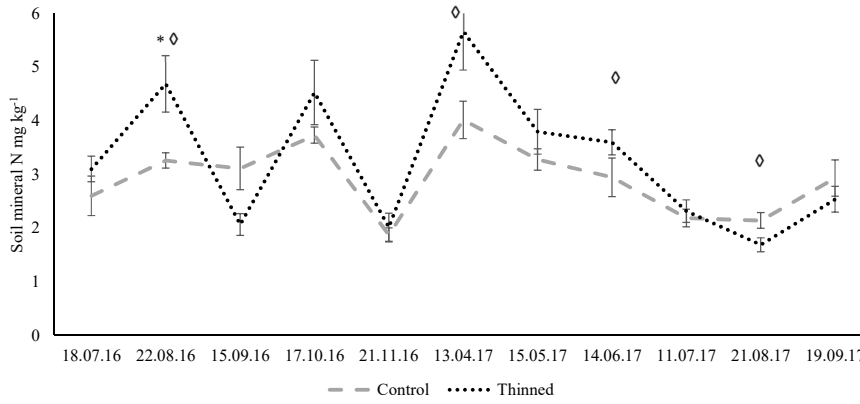
Table 2. Main soil characteristics for the study sites; N – Kjeldahl nitrogen, P – available (AL) phosphorus, K – available (AL) potassium, Ca – available calcium and Mg – available magnesium.

Stand and soil type (WRB 2006)	Soil layer depth (cm)	pH_{KCl}	N	Organic matter	P	K	Ca	Mg	Bulk density	N storage
			%		mg kg^{-1}				kg m^{-3}	t ha^{-1}
Silver birch (*Glossic Podsolnvizol*)	Control									
	0-10	5.5	0.11	2.7	64.2	163.9	633.3	115.7	1.25	1.38
	10-20	5.3	0.08	1.7	51.7	106.0	530.3	79.1	1.37	1.10
	20-30	5.7	0.07	1.4	53.8	98.6	591.1	82.4	1.44	1.01
	Thinned									
	0-10	5.5	0.12	3.0	83.6	140.4	709.1	125.1	1.20	1.44
	10-20	5.5	0.09	2.0	70.1	96.6	604.8	91.3	1.39	1.25
	20-30	5.4	0.08	1.6	55.7	76.3	555.7	64.3	1.47	1.18
Scots pine (*Gleyic Podzol*)	Control									
	0-10	3.8	0.13	5.6	33.5	45.3	98.3	10.9	0.91	1.18
	10-20	4.2	0.08	3.7	29.3	32.2	77.1	5.4	1.20	0.96
	20-30	4.2	0.05	2.3	25.0	25.0	59.5	1.8	1.20	0.60
	Thinned									
	0-10	3.8	0.11	4.3	34.2	29.3	112.1	11.0	0.90	0.99
	10-20	4.0	0.08	3.4	34.3	33.0	95.9	8.2	1.20	0.96
	20-30	4.2	0.05	2.0	30.5	35.4	67.9	12.4	1.20	0.60

Table 3. Annual net nitrification, net ammonification and total net mineralization (NNM), (kg ha^{-1} yr^{-1}) fluxes in the 0-10 cm topsoil layer of the silver birch and Scots pine stands.

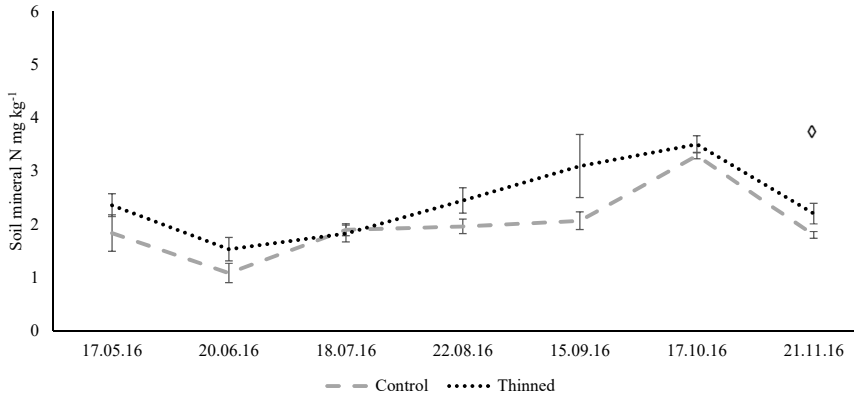
	Net nitrification	Share, %	Net ammonification	Share, %	Net N mineralization
			Silver birch		
Control, 2004-2005 yr*	59.50	60	39.50	40	99.00
Control, 2014-2015 yr	38.29	73	13.81	27	52.11
Control, 2016-2017 yr	14.20	48	15.62	52	29.82
Thinned, 2016-2017 yr	40.05	74	13.86	26	53.91
			Scots pine		
Control	0.01	0.05	19.43	99.95	19.44
Thinned	0.02	0.10	20.29	99.90	20.31

**Uri et al., 2008*



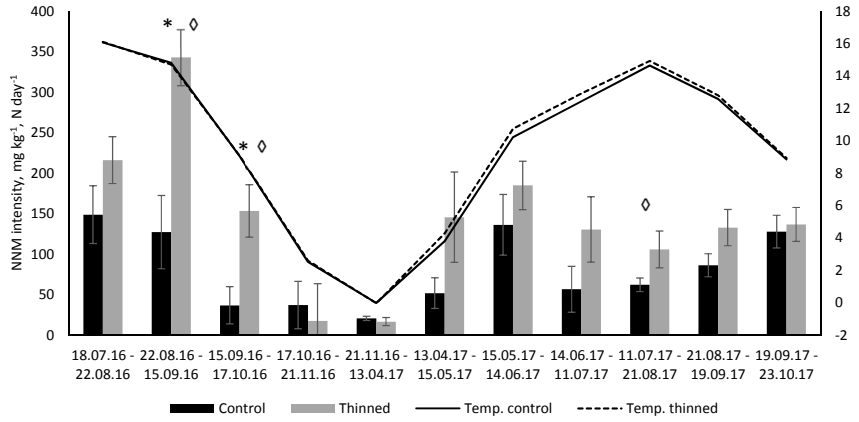
* - statistically significant difference (two-tail); ◊ - statistically significant difference (one-tail)

Figure 1. Dynamics of mean soil mineral nitrogen (NO^{-}_{3} + NH^{+}_{4}) content in the upper 10 cm soil layer of the silver birch stand. Bars indicate standard error (SE).



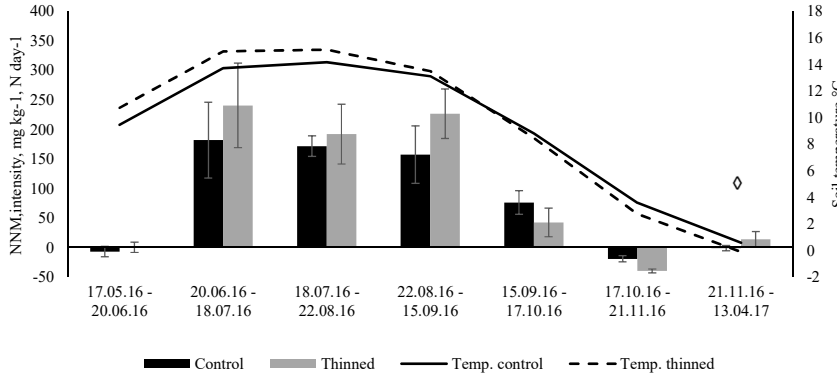
◊ - statistically significant difference (one-tail)

Figure 2. Dynamics of mean soil mineral nitrogen (NO^{-}_{3} + NH^{+}_{4}) content in the upper 10 cm soil layer of the Scots pine stand. Bars indicate standard error (SE).



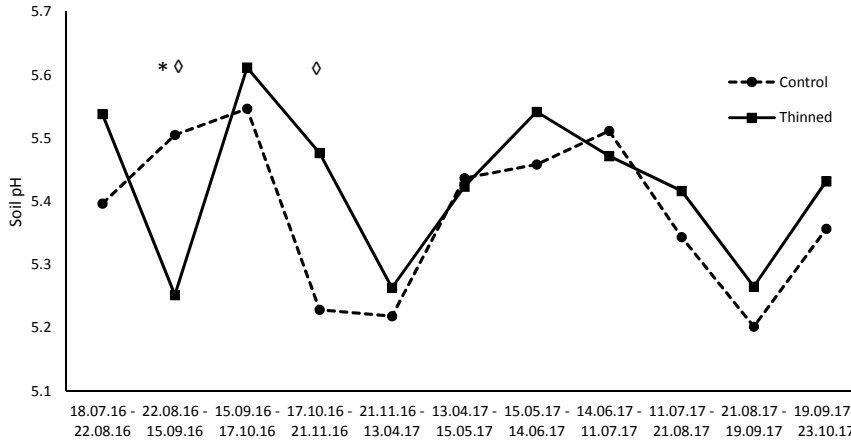
* - statistically significant difference (two-tail); ◊ - statistically significant difference (one-tail)

Figure 3. Dynamics of net nitrogen mineralization intensity (mg kg^{-1} N day^{-1}) and soil temperature in the upper 10 cm soil layer of the silver birch stand, control *versus* thinned. Bars indicate standard error.



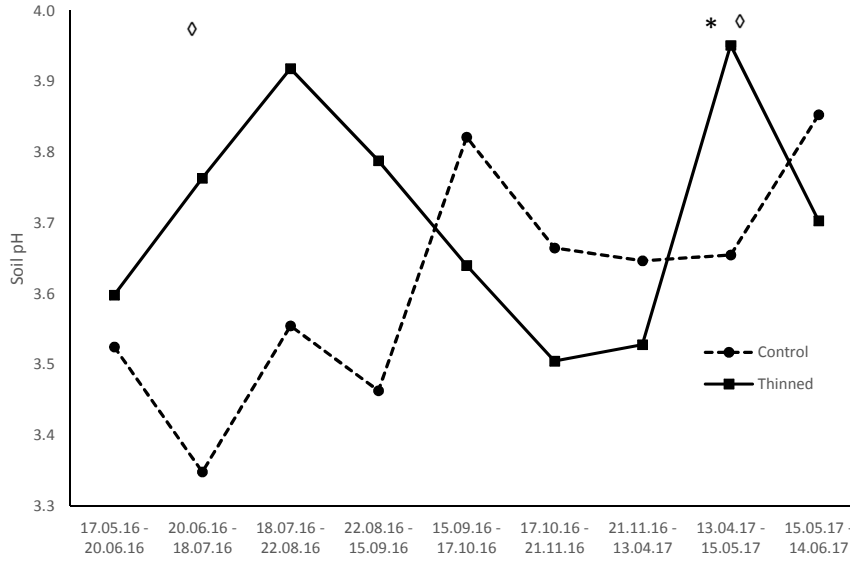
◊ - statistically significant difference (one-tail)

Figure 4. Dynamics of net nitrogen mineralization intensity (mg kg^{-1} N day^{-1}) and soil temperature in the upper 10 cm soil layer of the Scots pine stand, control *versus* thinned. Bars indicate standard error.



* - statistically significant difference (two-tail); ◊ - statistically significant difference (one-tail)

Figure 5. Dynamics of soil pH in the upper 10 cm soil layer of the thinned and control plots of the silver birch stand.



* - statistically significant difference (two-tail); ◊ - statistically significant difference (one-tail)

Figure 6. Dynamics of soil pH in the upper 10 cm soil layer of the thinned and control plots of the Scots pine stand.

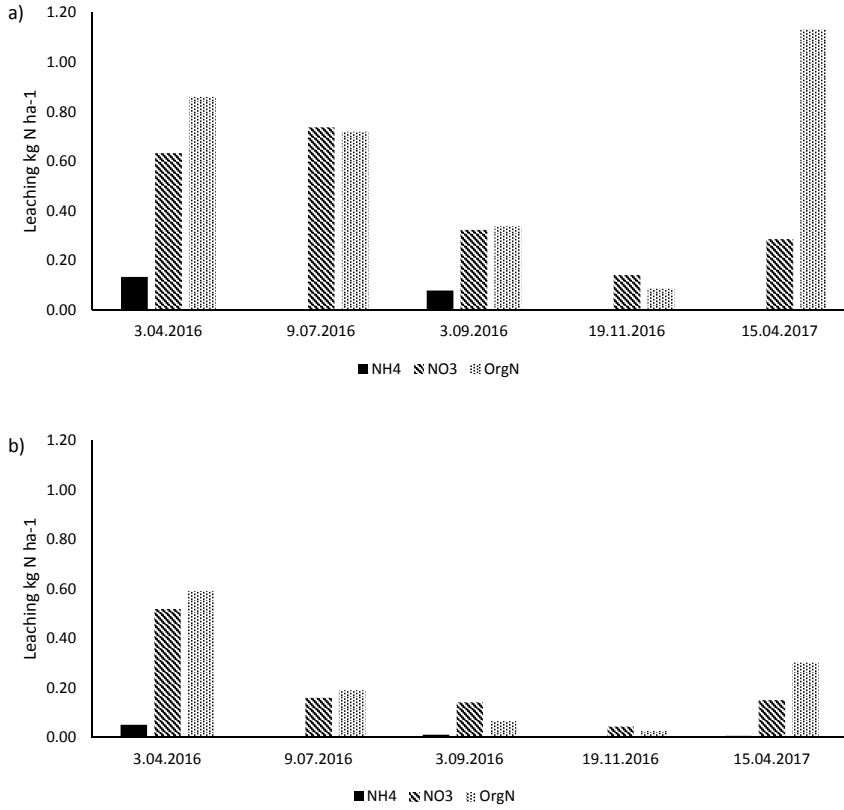


Figure 7. Dynamics of the leaching of the different forms of N in the silver birch stand, control (a) versus thinning (b).

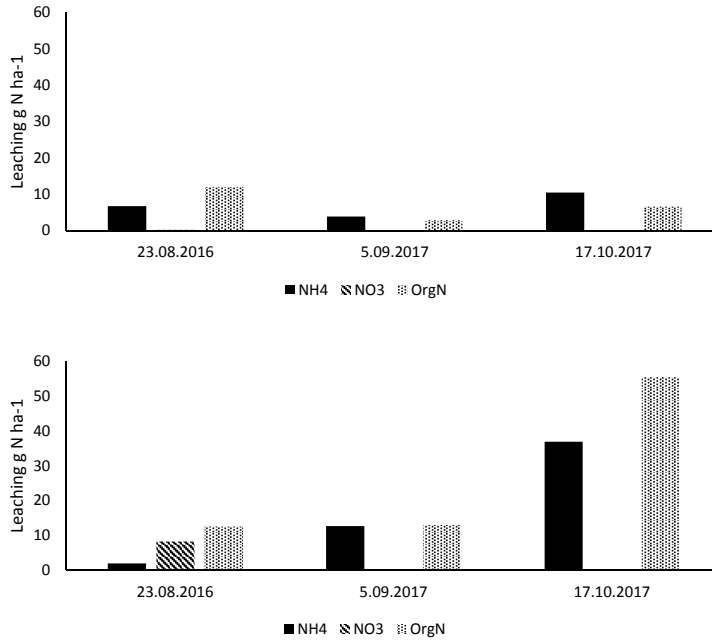


Figure 8. Dynamics of the leaching of the different forms of N in the Scots pine stand, control (a) versus thinning (b).

Appendix 1

Table A 1. Soil temperature and means of volumetric water content in the silver birch stand and difference in the means using Welch t-test, control versus thinned.

Period	Soil temperature °C			Soil moisture (VWC %)		
	Control	Thinned	p	Control	Thinned	p
18.07-22.08.16	16.1	16.1	0.91	25.6	10.4	**<0.01**
22.08-15.09.16	14.8	14.7	0.76	21.3	6.5	**<0.01**
15.09-17.10.16	9.1	9.1	0.98	12.8	4.7	**<0.01**
17.10-21.11.16	2.5	2.6	0.78	27.3	15.9	**<0.01**
21.11.16-13.04.17	0.0	0.0	0.94	33.2	22.5	**<0.01**
13.04-15.05.17	3.8	4.3	0.30	36.0	36.0	1.00
15.05-14.06.17	10.2	10.8	0.16	28.9	27.2	**0.05**
14.06-11.07.17	12.4	12.9	**<0.01**	29.1	21.5	**<0.01**
11.07-21.08.17	14.6	14.9	0.23	22.0	12.4	**<0.01**
21.08-19.09.17	12.6	12.8	0.44	31.4	25.1	**<0.01**
19.09-23.10.17	8.8	8.9	0.86	35.8	32.1	**<0.01**

Table A 2. Soil temperature and means of volumetric water content in the Scots pine stand and the difference in the means using Welch t-test, control versus thinned.

Period	Soil temperature °C			Soil moisture (VWC %)		
	Control	Thinned	p	Control	Thinned	p
17.05-20.06.16	9.5	10.8	**<0.01**	5.3	9.9	**<0.01**
20.06-18.07	13.7	15.0	**<0.01**	7.2	16.1	**<0.01**
18.07-22.08	14.2	15.1	**<0.01**	6.9	14.5	**<0.01**
22.08-15.09	13.1	13.5	0.27	7.1	16.5	**<0.01**
15.09-17.10	8.8	8.5	0.48	6.7	16.0	**<0.01**
17.10-21.11	3.6	2.7	**<0.01**	9.7	23.8	**<0.01**
21.11-20.12	1.5	0.6	**<0.01**	11.4	25.2	**<0.01**
20.12.16-19.01.17	0.8	0.0	**<0.05**	8.6	18.6	**<0.01**
19.01-18.02	-0.6	-1.3	**<0.01**	6.0	12.4	**<0.01**
18.02-17.03	-0.6	-0.9	**<0.01**	6.8	14.0	**<0.01**
17.03-13.04	1.7	1.0	0.10	7.4	17.9	**<0.01**

Appendix 2

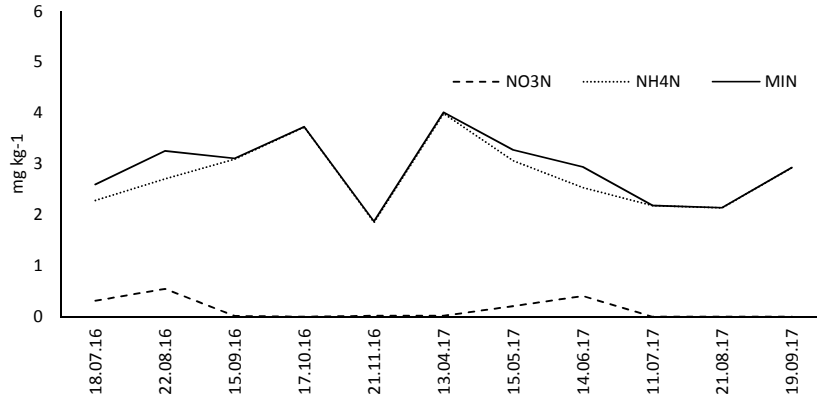


Figure A 1. Dynamics of mean concentrations of the different forms of mineral nitrogen (NO^{-}_{3} ; NH^{+}_{4}) in the upper 10 cm soil layer at the silver birch stand (control plot), (mean ± SE).

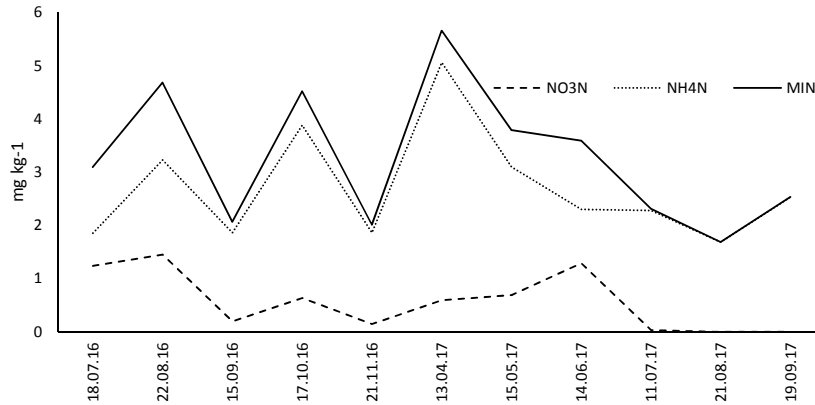


Figure A 2. Dynamics of mean concentrations of the different forms of mineral nitrogen (NO^{-}_{3} ; NH^{+}_{4}) in the upper 10 cm soil layer in the silver birch stand (thinned plot), (mean ± SE).

CURRICULUM VITAE

First name:	Gunnar
Surname:	Morozov
Citizenship:	Estonian
Date of birth:	22.09.1986
Address:	Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, 51014 Tartu, Estonia
Telephone:	+372 5668 9865
E-mail:	Gunnar.morozov@emu.ee

Education:

2014-2019	PhD studies in forestry, Institute of Forestry and Rural Engineering, Estonian University of Life Sciences
2012-2014	Master studies in forestry, Institute of Forestry and Rural Engineering, Estonian University of Life Sciences
2009-2012	Bachelor studies in forestry, Institute of Forestry and Rural Engineering, Estonian University of Life Sciences
2005-2008	Bachelor studies in economics, Faculty of Economics, University of Tartu
1998-2005	Tartu Raatuse Gymnasium
1997-1998	Tartu Descartes Lyceum
1993-1997	Tartu Kivilinna Gymnasium

Professional employment:

2015-…	Estonian University of Life Sciences, Institute of Forestry and Rural Engineering, Chair of Silviculture and Forest Ecology; specialist

Academic degree:

2012	MSc in forest management for the thesis: „ The growth development of curly birch (*Betula pendula* var. *carelica*) plantation and its dependence on the conditions of the soil and water regime “

Research interests:

silviculture, nutrient cycles in ecosystems, forest ecology, broadleaved short-rotation forestry, carbon in forest ecosystem

Foreign languages:

English, German, Russian

Training and special courses:

2016	The ELLS EU 4th Summer School – "Soil and Water", EGE University, Izmir, Turkey
	COST Training School - „Coppice economy – from planning to harvest", Mendel University, Brno, Czech Rep.
	Trees and shrubs under short rotation management: ecological and financial benefits and constraints, Latvia University of Agriculture (LUA)
2015	GCUA Graduate Summer School "The future of forests – Managing forests for people", Svergies lantbruksuniversitet (SLU)

Awards:

2016	RMK (State Forest Management Centre) Endel Laas scholarship for PhD students
2013	Estonian World Council, inc. Margot M. and Herbert R. Linna's scholarship
2013	RMK (State Forest Management Centre) Heino teder scholarship for master degree students
2012	RMK (State Forest Management Centre) Heino teder scholarship for master degree students
2012	Estonian Research Council, thank you certificate of the national student research competition in bio- and environmental sciences for the bachelor's thesis

Projects:

2017-2018	P170053MIMK. Estonian University of Life Sciences base funding topic. Effective and sustainable forest management. Investigator.
2016-2018	8T160024MIMK. Environmental Investment Center. Carbon budget in Scots pine chronosequence stands. Research staff.

2015-2018	8-2/T15078MIMK. State Forest Management Centre. Effect of clear-cut and thinning on forest carbon cycling. Research staff.
2015-2016	8-2/T15013MIMK. Environmental Investment Center. Carbon budgets in Silver birch-Norway spruce mixed stands. Research staff.
2014-2018	8-2/T14146MIMK. Estonian Environment Agency. Monitoring and modelling of forest litter in Estonia. Research staff.
2013-2015	1-18/113 T13072MIMK State Forest Management Centre. Carbon and nitrogen cycling in drained forests. Research staff.
2012-2015	ETF grant Nr. 9342. Estonian Science Foundation, Estonian Research Council. Potential environmental effects in relation to management of grey alder stands. Research staff.

ELULOOKIRJELDUS

Eesnimi:	Gunnar
Perekonnanimi:	Morozov
Kodakondsus:	Eesti
Sünniaeg:	22.09.1986
Aadress:	Metsandus- ja maaehitusinstituut, Eesti Maaülikool, Kreutzwaldi 5, 51014 Tartu
Telefon:	+372 5668 9865
E-mail:	Gunnar.morozov@emu.ee

Hariduskäik:

2014-2019	Eesti Maaülikool, metsandus- ja maaehitusinstituut, metsanduse eriala, doktoriõpe
2012-2014	Eesti Maaülikool, metsandus- ja maaehitusinstituut, metsamajanduse eriala, magistriõpe
2009-2012	Eesti Maaülikool, metsandus- ja maaehitusinstituut, metsamajanduse eriala, bakalaureuseõpe
2005-2008	Tartu Ülikool, majandusteaduskond, majandusteadus, bakalaureuseõpe
1998-2005	Tartu Raatuse Gümnaasium
1997-1998	Tartu Descartes'i Lütseum
1993-1997	Tartu Kivilinna Gümnaasium

Teenistuskäik:

2015-…	Eesti Maaülikool, metsandus- ja maaehitusinstituut, metsakasvatuse ja metsaökoloogia õppetool, spetsialist

Teaduskraad:

2012	magister metsamajanduse erialal. Magistritöö: „Kasvukeskkonna ja laasimise mõju maarjakase (*Betula pendula* var. *carelica*) kloonitaimede juurdekasvule kuivendatud mineraal- ja turvasmuldadel." Eesti Maaülikool

Teadustöö põhisuunad:

metsakasvatus, toitainete ringed ökosüsteemides, metsaökoloogia, kiirekasvulised lehtpuud, süsinik metsaökosüsteemis

Võõrkeelte oskus:

inglise, saksa, vene

Täiendkoolitused:

2016	The ELLS EU 4th Summer School – "Soil and Water", EGE University, Izmir, Turkey
	COST Training School - „Coppice economy – from planning to harvest", Mendel University, Brno, Czech Rep.
	Trees and shrubs under short rotation management: ecological and financial benefits and constraints, Latvia University of Agriculture (LUA)
2015	GCUA Graduate Summer School "The future of forests – Managing forests for people", Svergies lantbruksuniversitet (SLU)

Tunnustused:

2016	RMK Endel Laasi nimeline stipendium
2013	Ülemaailmse Eesti Kesknõukogu Margot M. ja Herbert R. Linna nimeline Stipendium
2013	RMK Heino Tederi nimeline stipendium
2012	RMK Heino Tederi nimeline stipendium
2012	SA Eesti Teadusagentuur, tänukiri bakalaureuseõppe üliõpilaste teadustööde riikliku konkursil bio- ja keskkonnateaduste valdkonnas

Projektid:

2017-2018	P170053MIMK. EMÜ baasfinantseerimisteema. Metsade keskkonnasäästlik ja efektiivne majandamine. Täitja.
2016-2018	8T160024MIMK. SA Keskkonnainvesteeringute Keskus. Süsinikubilanss palumännikute vanusereas. Põhitäitja.

2015-2018	8-2/T15078MIMK. Riigimetsa Majandamise Keskus. Raiete mõju metsade süsinikuringele. Põhitäitja.
2015-2016	8-2/T15013MIMK. SA Keskkonnainvesteeringute Keskus. Süsinikubilanss kuuse-kase segametsade vanusereas. Põhitäitja.
2014-2018	8-2/T14146MIMK. Keskkonnaagentuur. Metsavarise seire, uuringud ja modelleerimine. Põhitäitja.
2013-2015	1-18/113 T13072MIMK Riigimetsa Majandamise Keskus. Süsiniku- ja lämmastikuringe muudetud niiskureziimiga metsades. Research staff.
2012-2015	ETF grant Nr. 9342. Sihtasutus Eesti Teadusfond, Sihtasutus Eesti Teadusagentuur. Hall-lepikute majandamisega kaasnevad võimalikud keskkonnamõjud. Põhitäitja.

LIST OF PUBLICATIONS

Publications indexed in the Thomson Reuters Web of Science database

1. Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., Aun, K., Krasnova, K., **Morozov, G.**; Ostonen, I., Mander, Ü., Lõhmus, K., Rosenvald, K., Kriiska, K., Soosaar, K. (2019). The carbon balance of a six-year-old Scots pine (*Pinus sylvestris* L.) ecosystem estimated by different methods. Forest Ecology and Management, 433: 248–262.

2. **Morozov, G.**, Aosaar J., Varik, M., Becker, H., Lõhmus, K., Padari, A., Aun, K., Uri, V. (2019). Long-term dynamics of leaf and root decomposition and nitrogen release in a grey alder (*Alnus incana* (L.) Moench) and silver birch (*Betula pendula* Roth.) stands. Scandinavian Journal of Forest Research, 34(1): 12–25.

3. Aosaar, J., Varik, M., Becker, H., **Morozov, G.,** Aun, K., Kukumägi, M., Padari, A., Uri, V. (2019). Soil respiration and nitrogen leaching decreased in grey alder (*Alnus incana* (L.) Moench) coppice after clear-cut. Scandinavian Journal of Forest Research, 1–42.

4. Becker, H., Aosaar, J., Varik, M., **Morozov, G.**, Aun, K., Mander, Ü., Soosaar, K., Uri, V. (2018). Annual net nitrogen mineralization and litter flux in well-drained downy birch, Norway spruce and Scots pine forest ecosystems. Silva Fennica, 52 (4): 1–18.

5. Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., Soosaar, K., **Morozov, G.**, Ligi, K., Padari, A., Ostonen, I., Karoles, K. (2017). Carbon budgets in fertile grey alder (*Alnus incana* (L.) Moench.) stands of different ages. Forest Ecology and Management, 396: 55–67.

6. Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., **Morozov, G.**, Karoles, K. (2017). Ecosystems carbon budgets of differently aged downy birch stands growing on well-drained peatlands. Forest Ecology and Management, 399: 82–93.

7. Becker, H., Aosaar, J., Varik, M., **Morozov, G**., Kanal, A., Uri, V. (2016). The effect of Norway spruce stump harvesting on net nitrogen mineralization and nutrient leaching. Forest Ecology and Management, 377: 150−160.

8. Aosaar, J., Mander, Ü., Varik, M., Becker, H., **Morozov, G**., Maddison, M., Uri, V. (2016). Biomass production and nitrogen balance of naturally afforested silver birch (Betula pendula Roth.) stand in Estonia. Silva Fennica, 50 (4): 1−19.

9. Becker, H., Uri, V., Aosaar, J., Varik, M., Mander, Ü., Soosaar, K., Hansen, R., Teemusk, A., **Morozov, G**., Kutti, S., Lõhmus, K. (2015). The effects of clear-cut on net nitrogen mineralization and nitrogen losses in a grey alder stand. Ecological Engineering, 85: 237−246.